



Marrying molecules and morphology: first steps towards a reevaluation of solariellid genera (Gastropoda: Trochoidea) in the light of molecular phylogenetic studies

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ABSTRACT

The assignment of species to the vetigastropod genus *Solariella* Wood, 1842, and therefore the family Solariellidae Powell, 1951, is complicated by the fact that the type species (*Solariella maculata* Wood, 1842) is a fossil described from the Upper Pliocene. Assignment of species to genera has proved difficult in the past, and the type genus has sometimes acted as a ‘wastebasket’ for species that cannot easily be referred to another genus. In the light of a new systematic framework provided by two recent publications presenting the first molecular phylogenetic data for the group, we reassess the shell characters that are most useful for delimiting genera. Shell characters were previously thought to be of limited taxonomic value above the species level, but this is far from the case. Although overall shell shape is not a reliable character, our work shows that shell characters, along with radular and anatomical characters, are useful for assigning species to genera. Sculpture of the early teleoconch (the region immediately following the protoconch) and the columella are particularly useful characters that have not been used regularly in the past to distinguish genera. However, even with the combination of all morphological characters used in this study (shell, radular and eye), a few species are still difficult to assign to genera and in such cases molecular systematic data are essential. In the present study, we discuss 13 genera—12 of which were recovered as well-supported clades in recent molecular systematic studies—and provide morphological characters to distinguish them. We describe several new taxa: *Chonospeira* n. gen. (referred to as ‘clade B’ in previous molecular systematic studies), *Phragmomphalina* n. gen. (*Bathymophila* in part in molecular systematic studies) and *Phragmomphalina vilvensi* n. sp. (type species of *Phragmomphalina* n. gen.). We synonymize *Hazuregyra* Shikama, 1962 with *Minolia* A. Adams, 1860, *Minolia subangulata* Kuroda & Habe, 1952 with *Minolia punctata* A. Adams, 1860 and *M. gemmulata* Kuroda & Habe, 1971 with *M. shimajiriensis* (MacNeil, 1960). We also present the following new combinations: *Bathymophila bairdii* (Dall, 1889), *B. dawsoni* (Marshall, 1979), *B. regalis* (Marshall, 1999), *B. wanganellica* (Marshall, 1999), *B. ziczac* (Kuroda & Habe in Kuroda, Habe & Oyama, 1971), *Chonospeira nuda* (Dall, 1896), *C. iridescens* (Habe, 1961), *C. ostreion* (Vilvens, 2009), *C. strobilos* (Vilvens, 2009), *Elaphriella corona* (Lee & Wu, 2001), *E. diplax* (Marshall, 1999), *E. meridiana* (Marshall, 1999), *E. olivaceostrigata* (Schepman, 1908), *E. opalina* (Shikama & Hayashi, 1977), *Ilanga norfolkensis* (Marshall, 1999), *I. pykte* (Vilvens, 2009), *I. zaccaloides* (Vilvens, 2009), *Minolia shimajiriensis* (MacNeil, 1960), *M. watanabei* (Shikama, 1962), *Phragmomphalina alabida* (Marshall, 1979), *P. diadema* (Marshall, 1999), *P. tenuiseptum* (Marshall, 1999), *Spectamen euteium* (Vilvens, 2009), *S. basilicum* (Marshall, 1999), *S. exiguum* (Marshall, 1999) and *S. flavidum* (Marshall, 1999).

INTRODUCTION

For most of the last century, the vetigastropod family Solariellidae Powell, 1951 was usually treated as a subfamily of Trochidae Rafinesque, 1815 (e.g. Knight *et al.*, 1960; Marshall, 1979; Quinn, 1979; Hickman & McLean, 1990). However, in the last two decades,

it has been given family-level status in systematic reviews (Bouchet *et al.*, 2005, 2017; Poppe, Tagaro & Dekker, 2006; Vilvens, 2009; de Barros, 2010; Vilvens, Williams & Herbert, 2014; Vilvens & Williams, 2016; Cavallari *et al.*, 2019), a decision supported by recent molecular phylogenetic studies (Williams, Karube & Ozawa, 2008; Williams, 2012; Williams *et al.*, 2013).

The molecular systematic study by Williams *et al.* (2013) included representatives of all but two of the currently accepted solariellid genera. The two missing genera, both from the Atlantic, were *Microgaza* Dall, 1881 and *Suavotrochus* Dall, 1924, although a specimen erroneously thought to belong to the latter was included. Type species were included for *Ilanga* Herbert, 1987 and *Minolia* A. Adams, 1860 and a representative from the species complex including the type species was included for *Spectamen* Iredale, 1924 (see discussion below). *Solariella maculata* Wood, 1842, the type species of the nominotypical genus *Solariella* Wood, 1842, cannot be included in molecular systematic studies as it is a fossil described from the Upper Pliocene (Coralline Crag at Sutton, England) (Glibert, 1957; Marquet, 1995; Fig. 1A, H). The difficulties of relating this fossil species with Recent solariellid taxa have been discussed by various authors (e.g. Herbert, 1987; Warén, 1993; Marshall, 1999). A second molecular phylogeny, focusing on the evolution of eye reduction in solariellids, added a further seven species, including *Microgaza rotella* (Dall, 1881), the type species of *Microgaza* (Sumner-Rooney *et al.*, 2016).

Combining the findings of both molecular systematic papers, a total of 12 well-supported clades were found in Solariellidae. Five clades correspond to known genera: *Ilanga*, *Microgaza*, *Spectamen*, *Minolia* and *Zetela* Finlay, 1926. Two clades, each corresponding to a new genus, have recently been described; *Arxellia* Vilvens, Williams & Herbert, 2014 (= clade A in Williams *et al.*, 2013) and *Elaphriella* Vilvens & Williams, 2016 (= clade C in Williams *et al.*, 2013). Clades were also identified that include species assigned to *Solariella* and *Archiminolia* Iredale, 1929, although no type species were included for these genera. Two clades were treated together as *Bathymophila* Dall, 1881 in the molecular systematic studies, but are treated here as separate genera; *Bathymophila* and the new genus *Phragmomphalina* (see description below). The final clade, clade B of Williams *et al.* (2013), is described as the new genus *Chonospeira* (see description below), thus all 12 clades identified in the molecular phylogenetic studies are now named genus-level taxa.

The aim of the present paper is to investigate the supraspecific taxonomic implications of the two molecular studies and in particular to provide morphological characters that distinguish genera and to reevaluate the significance of shell morphology at the generic level as a source of informative taxonomic characters. The latter is particularly important, as many species have been described entirely on the basis of shell characters and historical type material often consists only of a dry, frequently damaged, shell.

Where genera have been recently described, or molecular systematic studies suggest little or no change to the current understanding of that genus, we refer the reader to the original description or recent monographs and make only a few comments. Where the generic concept based on molecular systematic data differs markedly from the traditional morphology-based concept, we focus on the characters of the species used in molecular systematic studies, highlighting those that are most informative. We list a brief and incomplete synonymy for some genera. Distributional data are provided using biogeographic zones (e.g. Indo-West Pacific, IWP; East Pacific), which in some cases correspond to oceans (Atlantic), unless more detailed data are available. Depth ranges given for genera are for living specimens where known. We follow Bouchet *et al.* (2008, p. 15) by taking the 'inner values' for any dredged samples to provide the most conservative estimate of depth range. Additional observations include general notes about the morphology of the eyes, as these data were included in both molecular systematic papers, as well as brief notes on shell colour. As shell shape alone is generally a poor predictor of generic assignment, we do not provide comprehensive species lists for all genera. Instead, we list species for which molecular data are available (indicated by an asterisk) and exemplar taxa for which confident generic assignment is possible on the basis of available shell and radular characters; a question mark is used to indicate assignments based on shell characters alone but where detailed examination was not possible, so assignment is

not completely certain; and fossil taxa are denoted by an obelus (†). Type species are shown in bold font. For new combinations, the previous generic assignments are listed in square brackets after the species name. Many solariellid species listed in online databases like MolluscaBase have been omitted from these lists because we have not had the opportunity to examine them in detail; this is particularly true for species assigned to the genus *Solariella*.

The work presented here is based on material from the following institutions: Australian Museum, Sydney (AMS); Atmosphere and Ocean Research Institute, University of Tokyo, Kashiwa (AORI); Florida Museum of Natural History, Gainesville, Florida (FLMNH); Louis Agassiz Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); Muséum national d'Histoire naturelle, Paris (MNHN); Natural History Museum, London (NHMUK); Museum of New Zealand Te Papa Tongarewa, Wellington (NMNZ); KwaZulu-Natal Museum, Pietermaritzburg (NMSA); National Museum of Nature and Science, Tokyo (NSMT); Swedish Museum of Natural History, Stockholm (SMNH); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM); Western Australian Museum, Perth (WAM); and Museum für Naturkunde, Berlin (ZMB).

SYSTEMATIC DESCRIPTIONS

Superfamily TROCHOIDEA Rafinesque, 1815

Family SOLARIELLIDAE Powell, 1951

Solariellinae Powell, 1951: p. 102 (type genus: *Solariella* Wood, 1842)

Minoliinae Kuroda, Habe & Oyama, 1971: p. 26 (type genus: *Minolia* A. Adams, 1860)

Description: Conchologically characterized by medium-sized, nacreous shells and anatomically by a terminal fringe around the oral disc (Fig. 1B, F, G). Protoconch varies little across the family; 1–1.5 whorls, with straight terminal margin and usually 5 or 6 (range is 3–9) spiral threads (Fig. 1C). Some species have additional microsculpture in the form of tiny beads. Radula short with *c.* 20–30 transverse rows of teeth; radula and radular sac straight and not coiled (Knight *et al.*, 1960; Herbert, 1987; Hickman & McLean, 1990). Anterior end of foot bilobed (Fig. 1G; Herbert, 1987: fig. 3). Cephalic tentacles often long and thick, especially in deeper-water species. Sensory papillae on cephalic tentacles much reduced compared with other trochoids (Hickman & McLean, 1990). Operculum corneous, thin and multispiral, with concentric nucleus. Eystalks much shorter than cephalic tentacles; eyes usually small with black pigment (Fig. 1B), except in some deep-water species, where they can be reduced and sometimes lack pigment, thus appearing to be completely absent when viewed under a dissecting microscope (e.g. species in *Bathymophila* and *Elaphriella*; Marshall, 1999; Williams *et al.*, 2013; Sumner-Rooney *et al.*, 2016).

Biology: The species of the family Solariellidae have a worldwide distribution, occurring in all oceans in polar, temperate and tropical waters on unconsolidated sediment. Although '*Solariella*' *varicosa* (Mighels & Adams, 1842) and '*Solariella*' *obscura* (Couthouy, 1838) vars *intermedia* (Leche, 1878) and *cinereaformis* (Leche, 1878) occur in depths as shallow as 5 m in the Kara Sea and Arctic Ocean (Warén, 1993), solariellids are most common on the outer shelf and continental slope (100–1,000 m depth) (Herbert, 1987; Williams, *et al.*, 2013). In the literature they are recorded from as deep as 4,100 m (Bagirov, 1995) and two of us have collected live specimens from > 2,400 m (*Bathymophila* sp., AW: no museum voucher; '*Machaeroplax*' *delicatus*, YK: AORI_YK#1959).

Species are dioecious. At least two South African species are known to brood young within the mantle cavity (Herbert, 1987); these are *Spectamen gerula* Herbert, 1987 and *S. multistriatum* (Thiele,

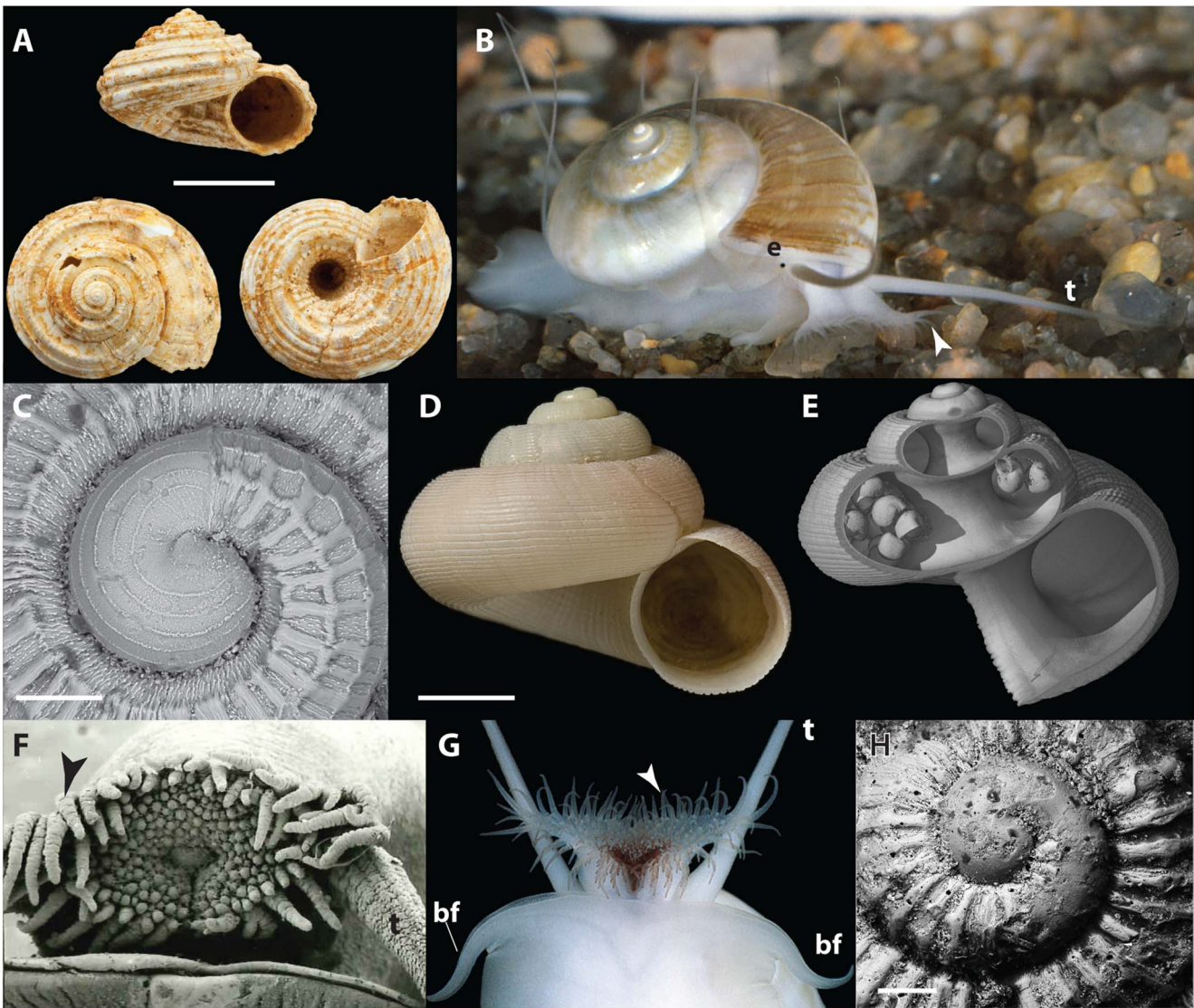


Figure 1. Solariellid characters. **A.** Syntype of *Solariella maculata* Wood, 1842, type species of *Solariella*. NHMUK G3956/2: Upper Pliocene from the Coralline Crag at Sutton, England (North Sea). Scale bar = 5 mm. **B.** A living specimen of solariellid *Ilanga laevisima* (von Martens, 1881). Modified from Herbert (1987). NMSA D4831: off Amanzimtoti, KwaZulu-Natal, South Africa, 100 m. **C.** Typical solariellid protoconch. *Solariella segersi* (Poppe, Tagaro & Dekker, 2006). MNHN IM-2007-18422: PANGLAO2005, CP2344, Bohol Sea, off Balicasag I., Philippines, 9°28.4'N, 123°50.1'E, 128–142 m. Scale bar = 100 μ m. **D.** South African *Spectamen multistriatum* (Thiele, 1925). NMSA V1208: off St Francis Bay, Eastern Cape, South Africa, 34°31'S, 25°21'E, 230–280 m. Scale bar = 2 mm. **E.** Computed tomography scan of the same specimen as in **D** with shell and soft tissues peeled away to show brood of juvenile shells present in the mantle cavity. **F.** Preserved specimen of *Microgaza rotella* (Dall, 1881). Note the fringe of finger-like projections surrounding the papillate oral disc. MNHN (no registration number): BIAÇORES, DP236, Azores Archipelago, south Sao Miguel, 37°22'N, 25°45'W, 470–500 m. **G.** Close-up of snout and bifurcated foot of living specimen of *Ilanga laevisima* viewed from below. Modified from Herbert (1987). NMSA D4831: off Amanzimtoti, KwaZulu-Natal, South Africa, 100 m. **H.** Syntype of *Solariella maculata*. Detail of protoconch. NHMUK G2050/3. Scale bar = 150 μ m. Abbreviations: e, eyes; t, tentacles; bf, bifurcated foot lobe. Arrows indicate finger-like projections around mouth in **B**, **F** and **G**. Photo credits: DGH and H. Taylor. Confocal image: L. Howard. SEM credits: AW and STW.

1925) (Fig. 1D, E). Herbert (1987) observed that these species possess a large protoconch (diameter 600–800 μ m) and, based on this character, it seems likely that this trait also occurs in other species. Possible candidates include *Spectamen roseapicale* Herbert, 1987 and *S. martensi* Herbert, 2015 (Herbert, 1987, 2015). New Zealand solariellids *Solariella plicatula* (Murdoch & Suter, 1906), and *S. luteola* (Powell, 1937) also have large protoconchs (diameter > 500 μ m) and are umbilical brooders (Marshall, 1999), as is the Japanese species *Hazuregyra watanabei* Shikama, 1962 (Hasegawa, 2009) (see below for new generic reassignment).

As in other vetigastropods, solariellids have eyes on short eyestalks next to the cephalic tentacles (Sumner-Rooney *et al.*, 2019).

Their eyes usually bear a pigmented, cup-shaped retina and a vitreous body that fills the retinal cup and acts as a lens (Ponder & Lindberg, 1997; Sasaki, 1998). Solariellid eyes tend to be small and Sumner-Rooney *et al.* (2016) concluded that functional eyes have been lost at least seven times within the Solariellidae and in at least three different ways in the 67 species examined; this has occurred through loss of pigmentation, obstruction of the eye aperture by epithelial tissue (withdrawal of eye into eyestalk) and degeneration of the vitreous body. Two morphologically distinct reduction pathways appear within two sister clades attributed to *Bathymophila* in Sumner-Rooney *et al.* (2016); these clades are treated as two distinct genera in this study.

Solariellids have rarely been studied in their natural habitat. However, available data show that some species are capable of swimming by rapid lateral movement of the foot (Herbert, 1987). They are thought to be opportunistic detritivores (Hickman & McLean, 1990; Warén, 1993). They live on soft sediment and are capable of rapid burrowing (Herbert, 1987). Some, although not all, species have patchy distributions suggesting that they may have highly specific ecological requirements (Marshall, 1999).

Fossils: We have very briefly looked into the palaeontological history of the solariellid genera. The assignment of the type species of *Solariella*, *S. maculata*, to Solariellidae is based primarily on the shape and size of its protoconch (400–500 µm) and early teleoconch sculpture (see comparison below). Moreover, the fauna accompanying *S. maculata* indicates a deep-water habitat (Marquet 1995), whereas species of Umboniinae and *Margarites* (which have similar shells) are usually found in shallow water (see comparison below).

Other fossil solariellid species include the three species used to calibrate the chronograms in the study by Williams *et al.* (2013): ‘*Solariella montsecana*’ from the Campanian of Torallola, Spain (Kiel & Bandel, 2001); *Solariella* sp. from the latest Oligocene part of the Lincoln Creek Formation in western Washington State, USA (Kiel, 2010; fig. 3C, D); and *Zetela awamoana* Laws, 1939, from the Mount Harris Formation, South Island, New Zealand (Beu & Raine, 2009). According to Williams *et al.* (2013), ‘*Solariella montsecana*’ (Vidal, 1921) shares some characters with *Arxellia*, but likely represents a distinct genus, *Solariella* sp. shares some characters with *S. anabilis* and *Z. awamoana* is a representative of the genus *Zetela*.

Additional fossil solariellid taxa include *Trochosolarium solarioides* (Seguenza, 1876) from the Italian Pliocene, which is very similar to *B. euspira* var. *nitens* (Dall, 1881); the generic name *Trochosolarium* may be a junior synonym of *Bathymophila*, but this needs further work. *Periaulax* Cossmann, 1888, which was based on the French Eocene fossil *Solarium spiratum* Lamarck, 1804, is another good candidate for inclusion in the Solariellidae. The type species of *Periaulax*, *P. spirata*, shares many shell characteristics with *Spectamen* (conical shell, flattened shoulders, spiral ribs on body whorl, beading around the umbilicus, spiral ribs on early whorls) and in overall shell shape it appears quite similar to the specimen used by Williams *et al.* (2013) under the name *S. philippense* and as such may be synonymous with *Spectamen* (for photographic images of several species assigned to this genus, including the type species, see the MNHN online catalogue for Palaeontology: <https://science.mnhn.fr/institution/mnhn/search>). More work is needed to clarify this issue; if the two names are synonyms, as the earlier name, *Periaulax* would have priority.

Comparison: Solariellids have often been confused with some genera in Seguenzioidea (e.g. *Calliotropis*) and even caenogastropod species, such as *Haloceras* (*Microphiliscus*) *constricta* (Dall, 1927), which was assigned to *Solariella* by Quinn (1979). More usually, solariellids are confused with members of the trochoid family Margaritidae and the trochid subfamily Umboniinae (see Table 1 for examples). Fortunately, all these groups differ from solariellids in their protoconch morphology. *Haloceras* has a multispiral protoconch consisting of protoconch I and II, with protoconch II having three keels (Warén & Bouchet, 1991); the sculpture of protoconch I consists of numerous microscopic riblets and pustules, which may coalesce to form 4–8 spiral cords (Warén & Bouchet, 1991). The umboniine protoconch differs from that of solariellids in being smaller (diameter ≤ 250 µm, usually 180–200 µm vs ≥ 350 µm in solariellids; Herbert, 1992) and possessing a fold, sometimes referred to as a ‘beak’ (Fig. 2B; Herbert, 1987, 1992). The protoconchs of other trochid species also tend to be small (<300 µm), have fewer spiral threads than most solariellids (usually 2–3) and many have a small constriction on the bulbous part of the protoconch (AW, pers. obs.); some like *Kaiparathina* species have strongly coloured protoconchs (not observed in solariellids). The protoconch of margaritids differs from solariellids in being low-set, flattened and usually smooth, with spiral ribs being absent

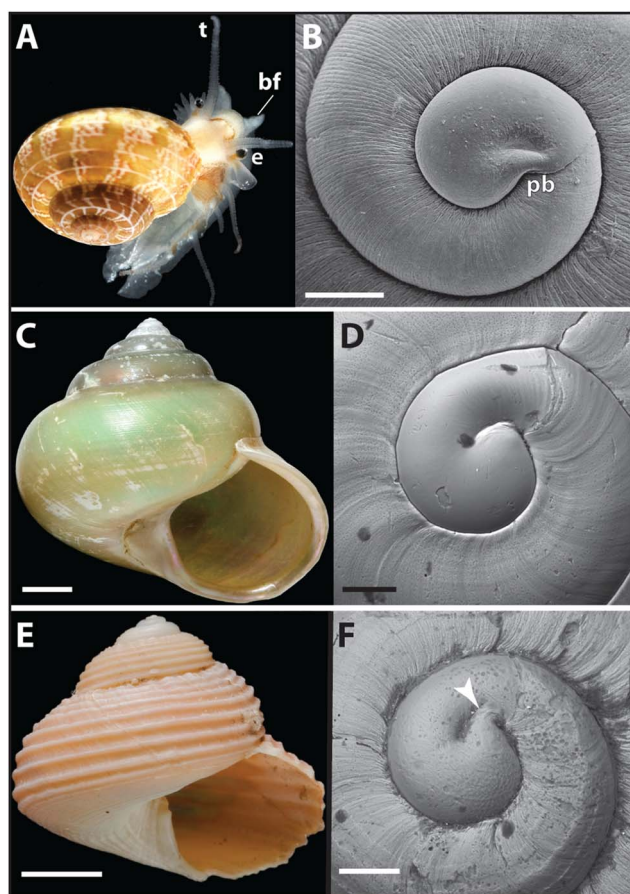


Figure 2. Non-solariellid taxa showing characters that differentiate them from solariellids. **A, B.** Trochid umboniine characters. **A.** Living umboniine (unidentified species). Note large eyes. MNHN: PAPUA NIUGINI, Sek Island, Papua New Guinea. **B.** *Pseudomimolia articulata* (Gould, 1861). Umboniine protoconch; note small size and ‘beak’. NMSA C7905: off Whale Rock, Eastern Cape, South Africa, 20–26 m. Scale bar = 100 µm. **C, D.** Characters of *Gaza*. **C.** Shell of *Gaza daedala* Watson, 1879. Note thickened and reflected outer shell lip indicating determinate growth. MNHN IM-2007-18293: AURORA, CP2682, Philippines, 15°01’N, 122°52’E, 1544–1624 m. Scale bar = 5 mm. Photo previously published by Williams (2012; fig. 1J). **D.** Protoconch of *Gaza* cf. *polychorona*. Note that the spiral ribs typical of solariellids are lacking. MNHN IM-2009-8872: TERRASSES, DW3122, Loyalty Ridge, New Caledonia, 23°35’S, 169°37’E, 660 m. Scale bar = 300 µm. **E, F.** *Margarites groenlandicus* (Gmelin, 1791). NHMUK 20110447: Isfjorden near Fuglefljellet Spitsbergen, Svalbard, Arctic Ocean, 78°12’46.5’’N, 15°14’7.5’’E, 8–13 m. **E.** Shell. Scale bar = 2 mm. **F.** Protoconch. Note small ‘bridge’ connecting bulbous initial part of protoconch to terminal edge. Scale bar = 100 µm. Abbreviations: e, eyes; t, tentacles; bf, bifurcated foot lobe; pb, protoconch beak. Photo credits: H. Taylor and L. Charles. SEM credits: DGH and STW.

(e.g. *Gaza*, Simone & Cunha, 2006; *Antimargarita*, Aldea, Zelaya & Troncoso, 2009; Fig. 2D); in *Margarites groenlandicus* (Gmelin, 1791) the bulbous part of the protoconch is connected by a small ‘bridge’ to just before the terminal edge of the protoconch (Fig. 2E, F). The margaritid protoconch may also comprise more whorls than the solariellid one (2 and 1–1.5, respectively) (Simone & Cunha, 2006) and may be eroded with a small hole at the apex (Simone & Cunha, 2006; Zhang & Zhang, 2017), a condition that is rare in solariellids.

Additional differences can also be used to separate Solariellidae and Margaritidae. Although the shells of margaritids overlap in size with solariellids, solariellids may be smaller: the shell length of most solariellids < 10 mm, whereas in margaritids it can exceed 20 mm (Hickman & McLean, 1990). The shell shape of margaritids tends towards equal length and width and does not include the lenticular or high spired shapes observed sometimes in solariellids; in the

SHELL CHARACTERS OF SOLARIELLID GENERA

Table 1. Status of genera that were originally, or at one time, considered to belong to Solariellidae or those that were based on species assigned originally to *Solariella*, but are no longer included in the family.

| Genus | Type species | Solariellid context | Current classification with reference |
|--|---|--|--|
| <i>Antisolarium</i> Finlay, 1926 | <i>Solarium egenum</i> Gould, 1849 | Finlay (1926) grouped this genus with the solariellids <i>Zeminolia</i> , <i>Zetela</i> and the fossil umboniine genus <i>Conominolia</i> . | Genus assigned to Umboniinae (Trochoidea: Trochidae) (Herbert, 1992). |
| <i>Bowdenagaza</i> † Woodring, 1928 | <i>Microgaza</i> (<i>Bowdenagaza</i>) <i>cossmanni</i> Woodring, 1928 | Described as a subgenus of <i>Microgaza</i> (Woodring, 1928). | Needs further study, possibly more closely related to trochid subfamily Umboniinae. |
| <i>Cidarina</i> Dall, 1909 | <i>Margarites cidaris</i> Carpenter, 1864 | Knight <i>et al.</i> (1960) assigned this genus to the Solariellinae. | Genus assigned to the Eucyclidae (Seguenzioidea) (Hickman & McLean, 1990). |
| <i>Ethaliopsis</i> Cossmann, 1918 | <i>Rotella zelandica</i> Hombron & Jacquinot, 1848 | Junior homonym of <i>Ethaliopsis</i> Schepman, 1908. | Replaced by <i>Zethalia</i> Finlay, 1926 (Trochoidea: Trochidae: Umboniinae). |
| <i>Helicoscala</i> Kuroda in Higo & Goto, 1993 | – | <i>Nomen nudum</i> | – |
| <i>Lirularia</i> Dall, 1909 | <i>Margarites lirulata</i> Carpenter, 1864 | Knight <i>et al.</i> (1960) assigned this genus as possibly belonging to the Solariellinae. Treated by Hickman & McLean (1990) as a member of the Solariellinae. | Genus assigned to the Umboniinae (Trochoidea: Trochidae) (Hickman & McLean, 1990; Williams <i>et al.</i> , 2008, 2010). |
| <i>Micropiliscus</i> Dall, 1927 | <i>Solariella</i> (<i>Micropiliscus</i>) <i>constricta</i> Dall, 1927 | Dall (1927) described <i>Micropiliscus</i> as a subgenus of <i>Solariella</i> ; this was followed by Quinn (1979). | Synonym of caenogastropod genus <i>Haloceras</i> Dall, 1889 (Vanikoroidea: Haloceratidae) (Warén & Bouchet, 1991). |
| <i>Monilea</i> Swainson, 1840 | <i>Trochus calliferus</i> Lamarck, 1822 | Pilsbry (1890) treated <i>Minolia</i> as a subgenus of <i>Monilea</i> . | Genus assigned to the Umboniinae (Trochoidea: Trochidae) (Hickman & McLean, 1990). |
| <i>Pseudotalopia</i> Habe, 1961 | <i>Pseudotalopia sakuraii</i> Habe, 1961 | Poppe, Tagaro & Dekker (2006) treated this as a solariellid genus. | Genus assigned to the Cantharidinae (Trochoidea: Trochidae) (Williams <i>et al.</i> , 2010; Williams, 2012). |
| <i>Solaricida</i> Dall, 1919 | <i>Solariella</i> (<i>Solaricida</i>) <i>hondoensis</i> Dall, 1919 | Described as subgenus of <i>Solariella</i> (Dall, 1919). | Synonym of <i>Calliotropis</i> Seguenza, 1903 (Seguenzioidea: Eucyclidae) (Hickman & McLean, 1990). |
| <i>Solariellopsis</i> Schepman, 1908 | <i>Solariellopsis calcarata</i> Schepman, 1908 | Schepman's (1908) placement of this genus is uncertain; he stated that the shell resembles <i>Solariella</i> , but that the radula is different. | A junior homonym of <i>Solariellopsis</i> de Gregorio, 1886, so is invalid. <i>Schepmanotropis</i> Poppe, Tagaro & Dekker (2006) is a replacement name. Now assigned to <i>Calliotropis</i> Seguenza, 1903 (Seguenzioidea: Eucyclidae) (WoRMS, 1 June 2018). |
| <i>Talopia</i> Gray, 1842 | <i>Trochus calliferus</i> Lamarck, 1822 | According to Finlay (1928) the Talopiidae is a mixed group of solariellids and umboniine trochids. | Synonym of <i>Monilea</i> Swainson, 1840 (Trochoidea: Trochidae: Umboniinae) (Hickman & McLean, 1990). |

Fossil taxa are denoted by ‘†’.

sculpture spiral ribs predominate (Hickman & McLean, 1990). Of the five genera currently recognized in the Margaritidae, *Margarites* comprises predominantly shallow-water species that do not have finger-like palps around the snout (Hickman & McLean, 1990). *Antimargarita* live in deeper water, but also lack digital projections around the snout (Aldea *et al.*, 2009). *Gaza*, *Anomphaloga* and *Callogaza* are similar to solariellids in being deep-water genera with finger-like papillae around the snout, but adult shells show determinate growth with a thickened and reflected shell lip (Fig. 2C; Hickman & McLean, 1990; Simone & Cunha, 2006; Hickman, 2012). In comparison to margaritids, the radula is shorter in solariellids (<30 rows) (Hickman & McLean, 1990).

The morphological and ecological similarities between the trochid subfamily Umboniinae and Solariellidae have been

discussed in some detail by Herbert (1992) so we list only the main points here. Umboniine species may have finger-like palps associated with the snout, but these usually occur subterminally on the sides of the snout (Herbert, 1992; Warén, 1993). In contrast, in solariellids longer projections are limited to a terminal fringe bordering the oral disc and the snout itself lacks longer projections (Fig. 1B, F). Although both solariellids and umboniines have an anteriorly bilobed foot, the shape differs: in umboniines it is somewhat constricted anteriorly before splitting into two trigonal projections (Herbert, 1992), whereas in solariellids it is not anteriorly constricted and the two lobes are long and thin (compare Figs 1G, 2A). Umboniines like solariellids have a short radula, but the teeth in the central field differ markedly with umboniines having a greatly reduced shaft and cusp (Herbert, 1992). Both groups occur

in unconsolidated sediment and both exhibit similar behaviour, with some species burrowing and swimming (Herbert, 1987, 1992). Umboniines do not occur at higher latitudes or in deep water and are found most commonly in the Indian and Pacific Oceans, where they occur at shallow depths, typically < 100 m, sometimes intertidally (Herbert, 1992). Most umboniine species have finer and longer asymmetric cephalic tentacles (right tentacle is longer; Hickman & McLean, 1990), often with more prominent sensory papillae and larger eyes (see Fig. 2A). Finally, we have noticed that in museum collections, samples of umboniine species often contain large numbers of individuals from a single locality (>50), even when collected offshore in dredges, suggesting higher population densities than we have observed for most solariellids.

See Table 1 for a list of genera that, although previously treated as solariellids, are no longer assigned to this family.

Remarks: Previous studies have suggested that shell characters alone are of limited value for assigning species to genera in the Solariellidae (e.g. Herbert, 1987; Warén, 1993; Marshall, 1999; Schwabe *et al.*, 2017) and most modern authors have relied heavily on radular characters to assign species to genera (Quinn, 1979; Herbert, 1987; Marshall, 1999). Williams *et al.* (2013), on the other hand, suggested that several genera occurring in the IWP are in need of systematic revision and that shell characters may prove useful to discriminate among clades defined on the basis of molecular systematic data. While we focus mainly on shell characters in this study, we also use radular characters. The number of epipodial tentacles has also been used as a supraspecific character in Solariellidae by some authors (Herbert, 1987), but others have suggested that it is of limited use as it can vary within a single species (Herbert, 1987) or even within a single individual (e.g. *Archimnolia oleacea* (Hedley & Petterd, 1906) has three right and four left epipodial tentacles; Marshall, 1999). Herbert (1987) argued that ontogenetic processes may account for differences in the number of epipodial tentacles between juvenile and adult specimens of some *Ilanga* species, but this has yet to be investigated.

Genus *Solariella* Wood, 1842

(Figs 1A, C, H, 3)

Solariella Wood, 1842: p. 531 (type species *Solariella maculata* Wood, 1842; by monotypy).

Machaeroplax Friele, 1877: p. 311 (type species *Machaeroplax affinis* Friele, 1877; by subsequent designation, Pilsbry, 1890: p. 307 in Pilsbry, 1889–1890).

Description: Due to imprecise generic concepts, many species, both non-solariellid and non-*Solariella*, have been incorrectly assigned to this genus. Our concept of *Solariella* includes species with the following characters; shell conical or turbinata in shape with flattened shoulders; first few teleoconch whorls sculpted with both spiral and axial ribs; peristome almost entire; columella curved and unornamented; interior of umbilicus unsculptured, or with spiral ribs that are sometimes beaded or plicate.

Additional observations: All *Solariella* species examined to date (*S. segersi*, *S. amabilis*, *S. chodon* and *Solariella* sp. 6 of Williams *et al.*, (2013)) have pigmented eyes with open apertures (Williams *et al.*, 2013; Sumner-Rooney *et al.*, 2016). Shells may be patterned with colours including yellow, pink and brown. Radular characters are unknown for the type species but *S. amabilis* (Jeffreys, 1865) (Fig. 3E) has well developed latero-marginal plates.

Distribution: IWP and Atlantic; living at 115–480 m (Warén, 1993; Williams *et al.*, 2013).

Comparison: Shells similar in overall shape to those of *Spectamen* and *Minolia*, but the sculpture of the early whorls in *Minolia* consists

of well-developed axial ribs, with the spiral sculpture being much weaker (at most spiral threads) or absent. Species assigned to *Spectamen* and *Solariella* in molecular systematic studies (Williams *et al.*, 2013) have been found to be sister to each other and are difficult to distinguish morphologically. The type species of *Solariella*, *S. maculata* (Fig. 1A, H), and all species of *Solariella* included in molecular systematic studies, have both axial and spiral ribs on the first few teleoconch whorls with axial ribs spanning the full (or nearly full) width of the whorl (Figs 1H, 3D). The axial ribs may start immediately after the protoconch or as late as the second whorl. Conversely, *Spectamen* does not have heavy axial ribs on the first whorl of the teleoconch, but axial pliculae may be evident later in shell growth, on the shoulder, where the axial sculpture does not span the full width of the whorl.

Remarks: Historically several North Atlantic species, especially *S. amabilis* (Jeffreys, 1865) (= *S. affinis* (Friele, 1877); Quinn, 1979; Warén, 1993), were thought to be typical of the genus. However, other species currently assigned to *Solariella* show only superficial similarity to the type species (Herbert, 1987; Warén, 1993; Marshall, 1999) and exhibit considerable diversity in shell shape and sculpture. More typical Recent examples may be found off the coast of West Africa; these are often considered to belong to lineages represented in Europe by Neogene fossil taxa (Bouchet, 1981; Warén, 1993). One possible example is *S. inoptanda* (Locard, 1898), an extant species from Western Sahara. Like the type species, *S. inoptanda* has distinctly shouldered whorls and the sculpture on the later whorls consists of relatively few, strong spiral cords, with finer intermediary spiral threads. Although *S. monodi* Fischer-Piette & Nicklès, 1946 has also been suggested as a possible descendent of *S. maculata* (Warén, 1993), it has a small, beaked protoconch and an axial sculpture of fine close-set striae. These characters in our view suggest that this species is an umboniine, possibly belonging to the genus *Lirularia*. Williams *et al.* (2013) included *S. amabilis* in their study (as *S. affinis*) and considered the clade including this species to be representative of the genus *Solariella*.

Machaeroplax is considered to be synonymous with *Solariella* by most authors (e.g. Odhner, 1912; Thiele, 1929; Marshall, 1979, 1999; Quinn, 1979; Herbert, 1987; Hickman & McLean, 1990; Warén, 1993). Intermediate forms with shell characters between those of *Solariella affinis*, the type species of *Machaeroplax*, and *S. amabilis*, which is a more strongly lirata form, suggest that *S. affinis* is synonymous with *S. amabilis*, a ‘true’ member of *Solariella* (Warén, 1993). In addition, Marshall (1979), on the basis of diagrams by Odhner (1912), suggested that the radula of *S. affinis* was not markedly different from *S. amabilis*. Williams *et al.* (2013) considered *S. affinis* to be genuinely representative of *Solariella*, so following them we maintain *Machaeroplax* as a synonym of *Solariella*. However, following Warén (1993), we treat *S. affinis* as a junior synonym of *S. amabilis* and thus refer to the specimen used in our study as *S. amabilis*. A Japanese species often assigned to *Machaeroplax* (*Machaeroplax delicatus* (Dall, 1919)) was also included in the study by Williams *et al.* (2013), but it did not cluster with *S. amabilis* and thus its generic affinities remain unclear.

Included species:

- **Solariella amabilis* (Jeffreys, 1865) (molecular data available only for form *affinis*);
- **S. chodon* Vilvens, 2009;
- †*S. cincta* (Philippi, 1836);
- S. inoptanda* (Locard, 1898);
- †*S. maculata* Wood, 1842;
- ?*S. multirestis* Quinn, 1979;
- **S. segersi* (Poppe, Tagaro & Dekker, 2006);
- **S. dedonderorum* (Poppe, Tagaro & Dekker, 2006);
- †*Solariella* sp. figure 3 in Kiel (2010) (used to calibrate molecular clock by Williams *et al.*, 2013);
- **Solariella* spp. 3, 4, 6 and 7 of Williams *et al.* (2013).

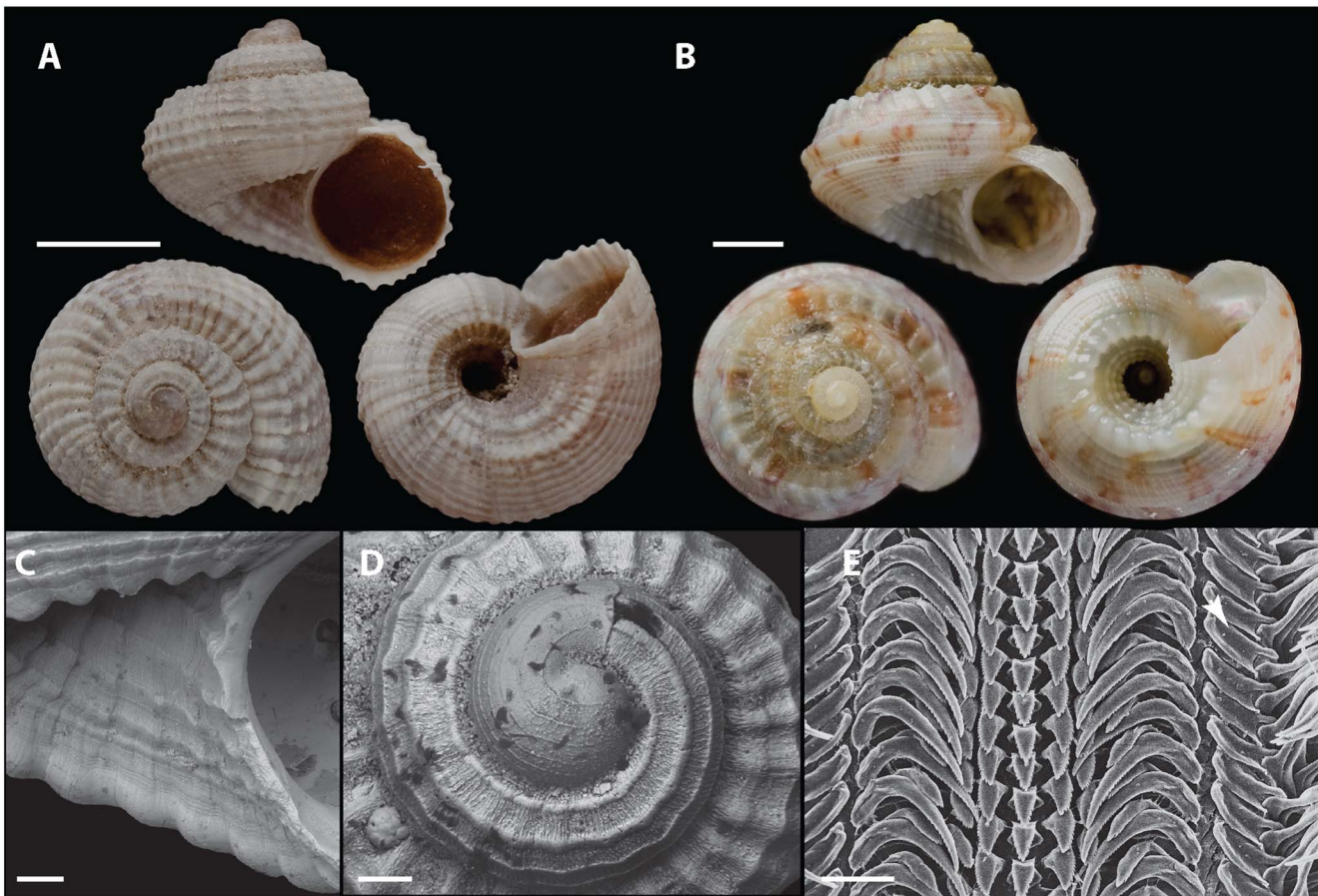


Figure 3. *Solariella* species used in molecular studies. **A.** *Solariella amabilis* (Jeffreys, 1865) form *affinis*. Species used in Williams *et al.*'s (2013) study as representative of the genus. NHMUK 20120233: Møre og Romsdal county, Vanylven, Rovdefjorden, NE of Kropperevet, Norway, 62°11.45'N, 5°34'E, 150–200 m. Scale bar = 1 mm. **B.** *Solariella dedonderorum* (Poppe, Tagaro & Dekker, 2006). MNHN IM-2007-18427: PANGLAO2005, DW2400, Bohol Sea, off Balicasag I., Philippines, 9°32.5'N, 123°41.8'E, 111–115 m. Scale bar = 1 mm. **C.** *Solariella dedonderorum*. Detail of columella and umbilical sculpture. MNHN IM-2007-18427. Scale bar = 200 μ m. **D.** *Solariella amabilis*. Protoconch and early whorls. NHMUK 20180166: Møre og Romsdal county, Vanylven, Rovdefjorden, NE of Kropperevet, Norway, 62°11.45'N, 5°34'E, 150–200 m. Scale bar = 100 μ m. **E.** *Solariella amabilis*. Radula showing latero-marginal plates (indicated by arrow). MNHN (no registration number): BALGIM, DR45, West Strait of Gibraltar, 35°44'N, 06°17'W, 293 m. Scale bar = 50 μ m. Photo credits: H. Taylor. SEM credits: STW and AW.

Genus *Archiminolia* Iredale, 1929

(Figs 4A, C–E, 5A)

Archiminolia Iredale, 1929: p. 170 (type species *Monilea oleacea* Hedley & Petterd, 1906; by original designation).

Description: Shell turbate with incomplete peristome (Fig. 4A). Interior of umbilicus with spiral ribs (Fig. 4C); columella slightly thickened, thickening most obvious in mid region and at base (Fig. 4C). Surface of columella roughened due to granular deposition of calcium carbonate (Fig. 5A). Whorls of early teleoconch usually have heavy spiral ribs, but no axial ribs (other than growth lines) (Fig. 4D). Spiral ribs may continue on to last adult whorl.

Additional observations: All *Archiminolia* species included in the studies by Williams *et al.* (2013) and Sumner-Rooney *et al.* (2016) with molecular data ($n = 3$) have pigmented eyes with open apertures. Molecular data are lacking for the type species, *A. oleacea*, but this species was examined in the study by Sumner-Rooney *et al.* (2016) and has unpigmented eyes and unknown apertural status, although the lack of eye pigment may be an artefact of preservation (Sumner-Rooney *et al.*, 2016). Shells may be patterned in colours such as pink and brown; on the body whorl colouring is often limited to the top half, with a clear demarcation between coloured and uncoloured areas. Radula with well-developed, elongate latero-marginal plates (Fig. 4E).

Distribution: IWP; living at 285–600 m (Williams *et al.*, 2013; Sumner-Rooney *et al.*, 2016).

Comparison: Species in this genus may be confused with the newly recognized genera *Elaphriella* (= clade C of Williams *et al.*, 2013) (Vilvens & Williams, 2016; Fig. 4) and *Phragmomphalina* n. gen. (= *Bathymophila* in part of Williams *et al.*, 2013), as well as *Bathymophila* and possibly *Ilanga*. *Elaphriella* differs most obviously from *Archiminolia* in that it has no spiral ribs inside the umbilicus and a thinner columella. In addition, while *Elaphriella* has no granular deposition of calcium carbonate on the columella, it usually has thin axial threads or fine striations (formed by microgranules) on the early teleoconch. *Archiminolia* differs from *Phragmomphalina* n. gen. and *Bathymophila* in lacking a callus or septum. Some *Bathymophila* specimens lack a callus, but these do not have spiral ribs inside the umbilical area. *Ilanga* has flatter, low-spired shells than *Archiminolia* and its radula lacks latero-marginal plates.

Remarks: The absence of eye pigment in *A. oleacea* had not been reported prior to the study by Sumner-Rooney *et al.* (2016); this is somewhat unusual as this species occurs in shallower depths than most species lacking functional eyes. *Archiminolia oleacea* was the only species studied by Sumner-Rooney *et al.* (2016) for which no material has been collected in the last 10 years, so it is possible that the pigment was lost as a result of differences in preservation methods or simply over time.

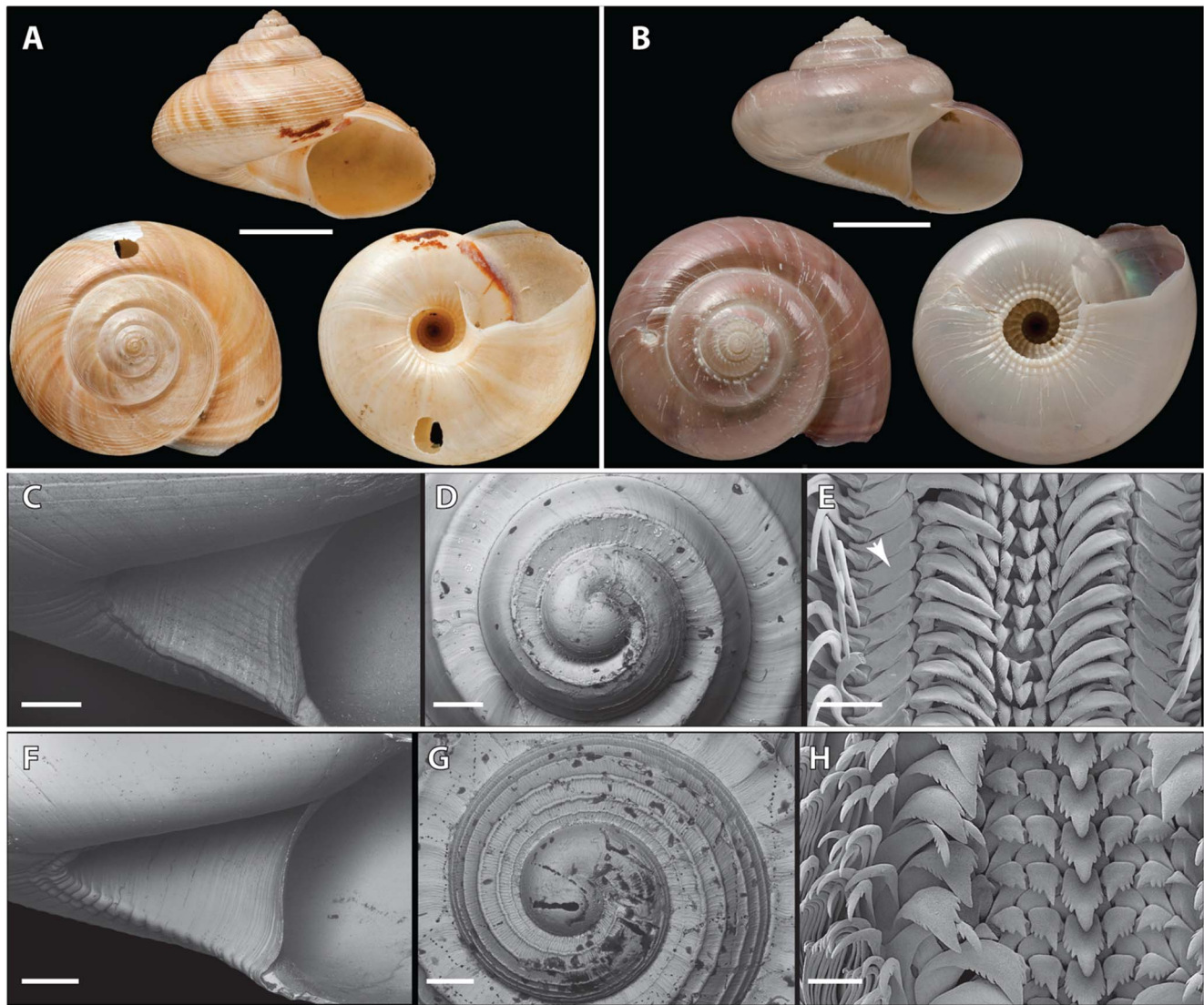


Figure 4. Comparison between *Archiminolia* and *Elaphriella*. **A.** Holotype of *Monilea oleacea* Hedley & Petterd, 1906, the type species of *Archiminolia*. AMS C024440: 23 miles E of South Head, Sydney, New South Wales, Australia, 33°51'S, 151°41.5'E, 457 m. **B.** Holotype of *Elaphriella cantharos* Vilvens & Williams, 2016, type species of *Elaphriella*. MNHN IM-2007-18534: SALOMON2, CP2243, W. Vella, Lavella I., Solomon Islands, 7°42.9'S, 156°27.3'E, 518–527 m. **C–E.** *Archiminolia oleacea*. **C.** Columella. Note thickened columella and spiral ribs inside umbilicus. AMS C024440. Scale bar = 1.5 mm. **D.** Protoconch and early whorls. Note spiral ribs and absence of axial ribs. AMS C363131: Capricorn Channel, NE of Lady Musgrave I., Queensland, Australia, 23°52'S, 152°42'E, 220 m. Scale bar = 150 µm. **E.** Radula. Note well-developed, elongate latero-marginal plates (indicated by arrow). Ex AMS C149644: off Maroochydore, S Queensland, Australia. Scale bar = 100 µm. **F–H.** *Elaphriella cantharos*. **F.** Columella. Note thinner columella and absence of spiral ribs inside umbilicus. MNHN IM-2007-18534. Scale bar = 1 mm. **G.** Protoconch and early whorls. Note spiral ribs and fine axial threads. MNHN IM-2007-1853. Scale bar = 150 µm. **H.** Radula. Note the absence of well-developed, elongate latero-marginal plates. MNHN IM-2009-15193: BIOPAPUA, CP3740, off Woodlark I., Papua New Guinea, 9°12'S, 152°16'E, 556–645 m. Scale bar = 20 µm. Photo credits: H. Taylor. SEM credits: STW and DGH.

Included species:

?*Archiminolia katoi* (Kuroda & Habe in Habe, 1961);

A. oleacea (Hedley & Petterd, 1906);

**Archiminolia* spp. 1 and 2 of Williams *et al.* (2013);

**Archiminolia* sp. 3 of Sumner-Rooney *et al.* (2016).

Genus *Arxellia* Vilvens, Williams & Herbert, 2014

(Figs 5C, 6A, C–E)

Arxellia Vilvens, Williams & Herbert, 2014: p. 258 (type species *Arxellia trochos* Vilvens, Williams & Herbert, 2014; by original designation).

Clade A Williams *et al.*, 2013.

Description: Shell robust and conical, with a straight profile and approximately as high as wide, or higher than wide; peristome incomplete (Fig. 6A). Shell nacreous; sometimes pigmented (usually brown), but often lacks pigmentation. Sculpture of first whorl of teleoconch consists of spiral ribs, sometimes with thin axial threads (Fig. 6D). Umbilical sculpture variable, but umbilicus always surrounded by beading (Fig. 6C). Columella thickened, usually reflected and thicker midway, sometimes with a small callus (Figs 5C, 6C). Granular deposition of calcium carbonate evident on columella (Fig. 5C). For more detail, see description by Vilvens *et al.* (2014).

Additional observations: All *Arxellia* species examined to date (*A. tracheia*, *A. helicoides*, *A. tenorioi*, *A. trochos* and *Arxellia* sp. 5) have pigmented

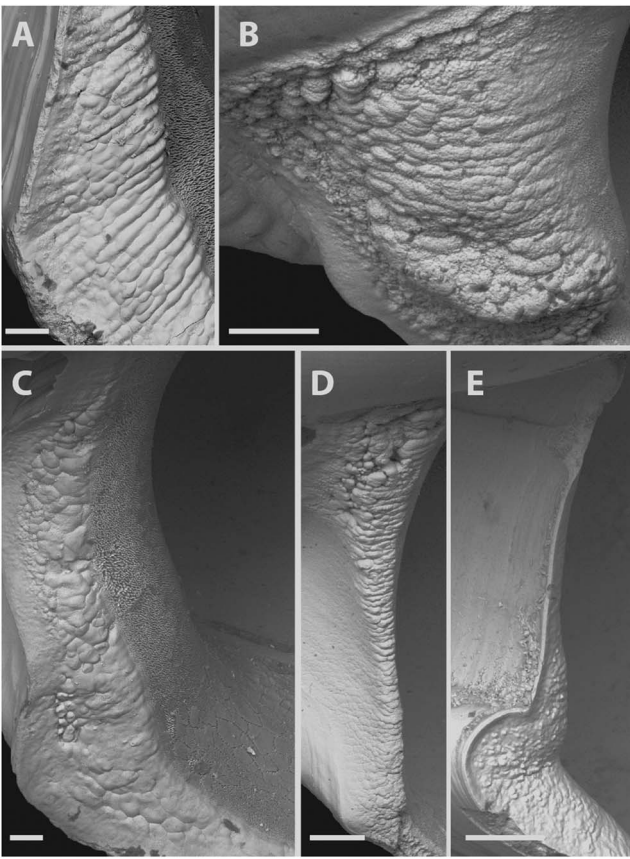


Figure 5. Granular deposition of calcium carbonate in five genera. **A.** *Archiminolia oleacea*. Note the presence of nacre inside the shell lip, giving the appearance of tiny prickles. AMS C133269.001: N of Fraser I., Queensland, Australia, 24°22.5'S, 153°17.1'E, 192–229 m. Scale bar = 100 µm. **B.** *Bathymophila* sp. 11 of Williams *et al.* (2013). MNHN IM-2009-15175: TARASOL, DW3369, Niau, Tuamotu Archipelago, 16°08'S, 146°24'W, 412–520 m. Scale bar = 200 µm. **C.** *Arxellia herosae* Vilvens, Williams & Herbert, 2014. MNHN IM-2009-28740: NORFOLK1, DW1691, Norfolk Ridge, Sponge Bank, New Caledonia, 24°54'S, 168°22'E, 509–513 m. Scale bar = 100 µm. **D.** *Phragmomphalina diadema* (Marshall, 1999). MNHN IM-2009-8869: TERRASSES, DW3045, Mont J, Loyalty Ridge, 23°48'S, 169°46'E, 660–710 m. Scale bar = 0.5 mm. **E.** *Microgaza rotella* (Dall, 1881). MNHN IM-2013-8023: KARUBENTHOS 2012, GD33, Guadeloupe, 16°24'N, 61°33'W, 130 m. Scale bar = 200 µm. SEM credits: STW.

eyes with open apertures (Williams *et al.*, 2013; Sumner-Rooney *et al.*, 2016). All species examined to date have soft tissues that exhibit some vivid blue colouration; sometimes this blue pigment can be seen through the shell, but its origin is unknown. Radula with well-developed, elongate latero-marginal plates (Fig. 6E).

Distribution: IWP; living at 242–650 m (Vilvens *et al.*, 2014).

Comparison: The robust, conical shells of *Arxellia* separate them from *Archiminolia*, *Elaphriella*, *Ilanga*, *Microgaza* and *Chonospeira* n. gen. and the absence of a callus or septum over the umbilicus separates them from *Phragmomphalina* n. gen. and most *Bathymophila*. Unlike *Arxellia*, *Bathymophila* species that lack a callus do not have beading around the umbilicus. Unlike *Minolia* and *Zetela*, *Arxellia* species lack heavy axial ribs on the early whorls of the teleoconch. Some *Solariella*, *Spec-tamen*, *Zetela* and *Suavotrochus* species may be similar in shell shape to *Arxellia*, but they do not have calcareous deposits on the columella.

Remarks: This genus was described by Vilvens *et al.* (2014) on the basis of the molecular systematic data of Williams *et al.* (2013), which showed the species included for *Arxellia* to be a well-supported

clade (clade A). Genetically, *Arxellia* is strongly supported as sister to *Archiminolia* (Williams *et al.*, 2013; Sumner-Rooney *et al.*, 2016) and these two genera share both radular characters and the deposition of granular calcium carbonate on the columella with *Phragmomphalina* n. gen. and *Bathymophila*. Sumner-Rooney *et al.* (2013) have shown that these four genera together with '*Bathymophila*' sp. 18 form a clade, suggesting that they share a common ancestor, but support for this clade was lacking (PP = 0.46). The type species of *Arxellia*, *Arxellia trochos*, was not included in the study by Williams *et al.* (2013), but was included in Sumner-Rooney *et al.*'s (2016) phylogenetic analysis, which confirmed the position of *A. trochos* among others referred to the genus *Arxellia*.

Included species:

- **Arxellia boucheti* Vilvens, Williams & Herbert, 2014;
- A. erythraea* Vilvens, Williams & Herbert, 2014;
- **A. helicoides* Vilvens, Williams & Herbert, 2014;
- **A. herosae* Vilvens, Williams & Herbert, 2014;
- A. maestratii* Vilvens, Williams & Herbert, 2014;
- **A. tenorioi* (Poppe, Tagaro & Dekker, 2006);
- **A. thaumasta* Vilvens, Williams & Herbert, 2014;
- **A. tracheia* Vilvens, Williams & Herbert, 2014;
- ****A. trochos* Vilvens, Williams & Herbert, 2014;**
- **Arxellia* sp. 5 of Williams *et al.* (2013).

Genus *Bathymophila* Dall, 1881

(Figs 5B, 6B, F–H, 7G, H)

Bathymophila Dall, 1881: p. 102 (type species *Margarita euspira* Dall, 1881; by monotypy).

Solariella (*Ethaliopsis*) Schepman, 1908: p. 51 (type species *Solariella* (*Ethaliopsis*) *callomphala* Schepman, 1908; by monotypy; not *Ethaliopsis* Cossmann, 1918 = *Zethalia* Finlay, 1926; synonymized with *Bathymophila* by Marshall, 1999).

Bathymophila Williams *et al.*, 2013; Sumner-Rooney *et al.*, 2016 (both in part; includes *Phragmomphalina* n. gen.).

Description: Shell usually wider than high, occasionally turbate but often flatter, with incomplete peristome (Figs 6B, 7G, H). Where observation is possible, no regular sculpture evident within umbilicus, although one species has a roughened surface (Williams *et al.*, 2013: *Bathymophila* sp. 5). Umbilicus usually covered with a thick callus (Figs 5B, 6B, F). Adults lacking a callus have a peri-umbilical ridge at base of columella, which may form a flange around the rim of the umbilicus (Fig. 7G). Patches of granular deposition of calcium carbonate occur over callus if present or on columella (Figs 5B, 6F). Sculpture of early teleoconch consists of heavy spiral ribs, sometimes with fine axial threads (Fig. 6G).

Additional observations: All species examined to date (*B. gravida* Marshall 1999, *B. callomphala* (Schepman 1908), *Bathymophila* spp. 6, 7, 9, 10, 11, 15, 16, 20) from this clade have unpigmented eyes (Marshall, 1999; Williams *et al.*, 2013; Sumner-Rooney *et al.*, 2016). Shells of deeper-water taxa are often unpigmented, but may have a pearly green or pink iridescence, especially when live-collected; some species have (usually faint) yellow, brown or pink pigmentation; *B. dawsoni* (Marshall, 1979), *B. cf. dawsoni* = *B.* sp. 12 in Williams *et al.* (2013), *B. regalis* (Marshall, 1999), *B. wanganellica* (Marshall, 1999) and *B. ziczac* (Kuroda & Habe in Kuroda, Habe & Oyama, 1971) are all similar in appearance and are the only species known to exhibit colour patterns (Fig. 7G). Radula with trigonal latero-marginal plates possessing a filament-like shaft and cusp (Marshall, 1999; Fig. 6H). Information on the radula of the type species is lacking.

Distribution: Predominantly IWP, but also Caribbean (*B. bairdii* (Dall, 1889)) and northeastern Atlantic (*B. euspira* and *B. micans* (Dautzenberg & Fischer, 1896)) (Quinn, 1979; Marshall, 1999; Williams *et al.*,

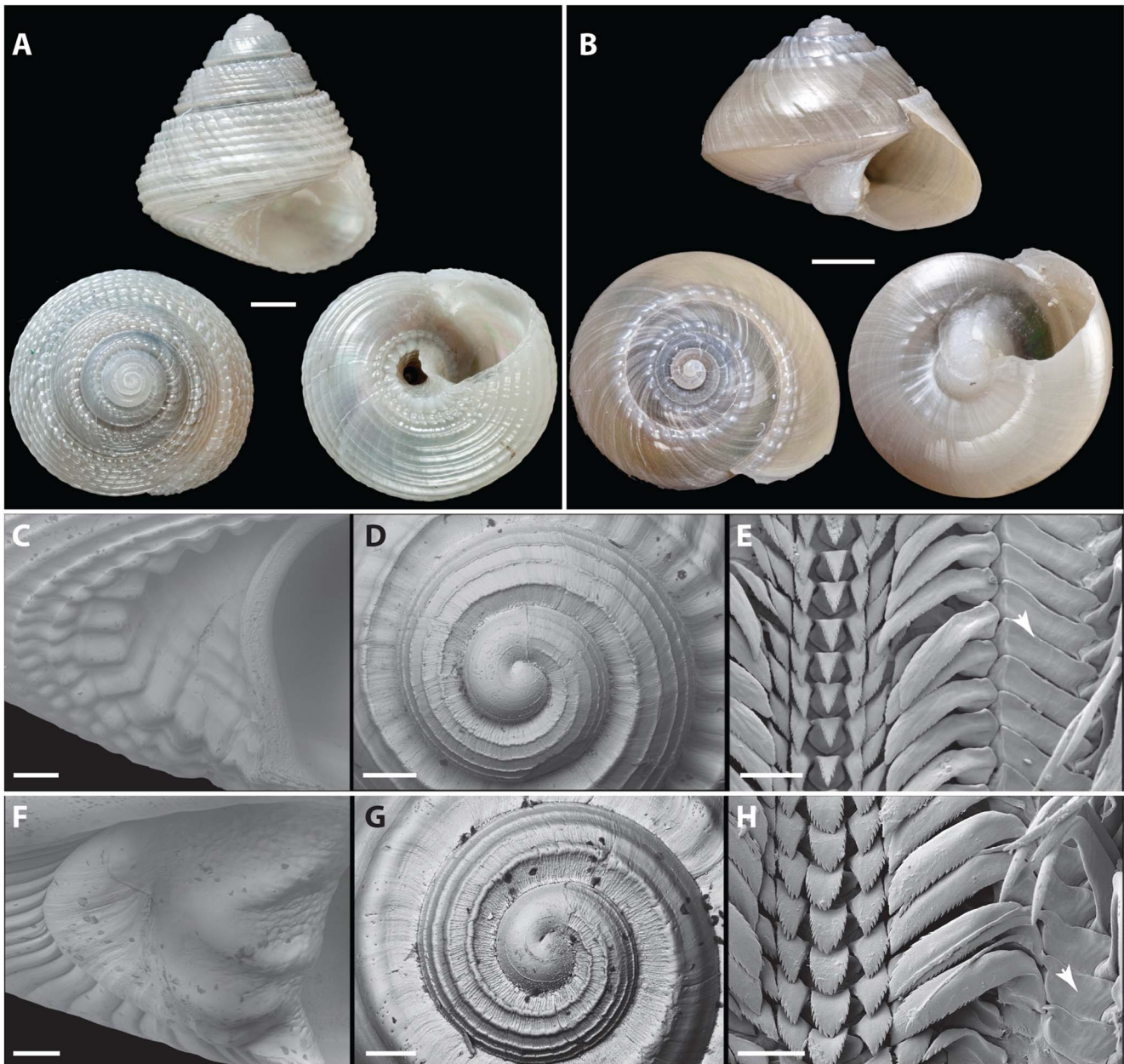


Figure 6. Comparison between *Arxellia* and *Bathymophila*. **A.** Holotype of *Arxellia trochos* Vilvens, Williams & Herbert, 2014, type species of *Arxellia*. MNHN IM-2009-23092: EXBODI, DW3862, Banc de L'Orne/Walpole, New Caledonia, 22°20'S, 169°01'E, 400–520 m. Scale bar = 1 mm. **B.** *Bathymophila* sp. 6 of Williams *et al.* (2013). MNHN IM-2009-23090: EXBODI, DW3938, Récif Pétrie, New Caledonia, 18°36'S, 164°24'E, 505–761 m. Scale bar = 1 mm. **C–E.** *Arxellia trochos*. **C.** Columella. Note thickened columella and granular deposition of calcium carbonate. MNHN IM-2009-23109: EXBODI, CP3851, Banc Sud Durand, New Caledonia, 22°19'S, 168°45'E, 471–510 m. Scale bar = 300 μ m. **D.** Protoconch and early whorls. Note spiral ribs on early teleoconch whorls. MNHN IM-2009-23109. Scale bar = 150 μ m. **E.** Radula. Note well-developed, elongate latero-marginal plates (indicated by arrow). MNHN IM-2009-23089: EXBODI, DW3862, Banc de L'Orne/Walpole, New Caledonia, 22°20'S, 169°01'E, 400–520 m. Scale bar = 50 μ m. **F–H.** *Bathymophila*. **F.** *Bathymophila* sp. 1 of Williams *et al.* (2013). Detail of columella. MNHN IM-2007-18313: EBISCO, CP2571, N Bellona, New Caledonia, 20°25'S, 158°45'E, 298–309 m. Scale bar = 300 μ m. **G.** *Bathymophila* sp. 11 of Williams *et al.* (2013). Protoconch and early whorls. MNHN-2009-15175: TARASOL, DW3369, Niau, Tuamotu Archipelago, 16°08'S, 146°24'W, 412–520 m. Scale bar = 150 μ m. **H.** *Bathymophila* sp. 20 of Williams *et al.* (2013). Radula. Note well-developed, elongate latero-marginal plates with a filament-like shaft and cusp (indicated by arrow). MNHN IM-2009-23082: EXBODI, DW3879, Ile Matthew-Volcan, New Caledonia, 22°19'S, 171°20'E, 925 m. Scale bar = 50 μ m. Arrows indicate latero-marginal plates. Photo credits: H. Taylor. SEM credits: STW and DGH.

2013; Sumner-Rooney *et al.*, 2016). *Bathymophila euspira* is recorded in the east Atlantic from depths as great as 2,003 m (Quinn, 1979; note this record may refer to *B. euspira* var. *nitens* (Dall, 1881)) and AW has collected live *B. euspira* var. *nitens* from 2,325 m from the Bay of Biscay (47°36.1'N, 08°40.5'W). Living at 133–2,325 m (Marshall, 1999; Williams *et al.*, 2013; this study).

Comparison: *Bathymophila* shares some shell characteristics with *Phragmomphalina* n. gen., *Archiminolia* and *Arxellia*. Most *Bathymophila* species differ from these three genera in having a heavy callus. In *Phragmomphalina* n. gen. the umbilicus is covered by a fragile septum, which is easily broken and shells are usually turritate. Some species of *Bathymophila* lack a callus (e.g. *Bathymophila*

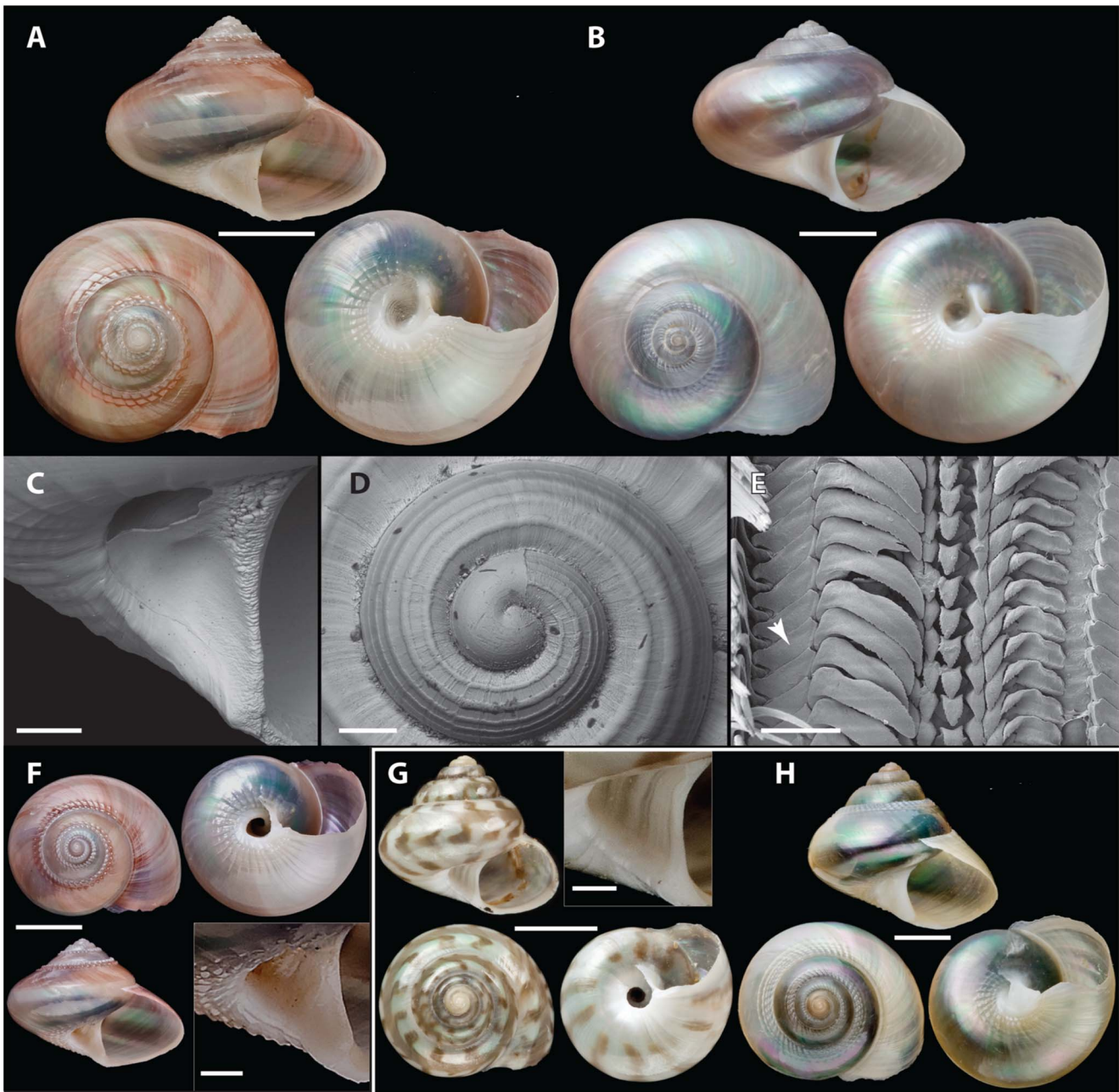


Figure 7. Comparison between *Phragmomphalina* n. gen. and *Bathymophila*. **A–F.** *Phragmomphalina* n. gen. **A.** Holotype of *Phragmomphalina vilvensi* n. sp. (= *Bathymophila* sp. 4 in Williams *et al.*, 2013), the type species of *Phragmomphalina* n. gen. MNHN IM-2009-8769: MIRIKY, CP3192, Between Nosy-bé and Banc du Leven, Madagascar, 12°26'S, 48°13'E, 578–782 m. Scale bar = 5 mm. **B.** *Phragmomphalina diadema* (Marshall, 1999). MNHN IM-2009-13010: SALOMON2, CP2249, NW Vella, Lavella I., Solomon Islands, 7°31.3'S, 156°17.7'E, 782–884 m. Scale bar = 5 mm. **C.** *Phragmomphalina diadema*. Detail of columella. MNHN IM-2009-8869: TERRASSES, DW3045, Loyalty Ridge, New Caledonia, 23°48'S, 169°46'E, 660–710 m. Scale bar = 1 mm. **D.** *Phragmomphalina vilvensi* n. sp. Protoconch and early whorls. MNHN IM-2009-8772: MIRIKY, CP3221, between Nosy-bé and Banc du Leven, Madagascar, 12°47'S, 48°08'E, 782 m. Scale bar = 150 µm. **E.** *Phragmomphalina vilvensi* n. sp. Radula with well-developed latero-marginal plates (indicated by arrow). MNHN IM-2009-8773: MIRIKY, CP3221, between Nosy-bé and Banc du Leven, Madagascar, 12°47'S, 48°08'E, 782 m. Scale bar = 100 µm. **F.** *Phragmomphalina vilvensi* n. sp. Specimen lacking a septum. MNHN IM-2009-8770: MIRIKY, CP3186, between Nosy-bé and Banc du Leven, Madagascar, 12°34'S, 48°09'E, 613–625 m. Scale bar = 5 mm; scale bar for inset = 1 mm. **G–H.** *Bathymophila*. **G.** *Bathymophila cf. dawsoni* (= sp. 12 of Williams *et al.*, 2013). Species lacking a callus. Note heavy rib at base of columella in inset. MNHN IM-2009-28741: BORDAU1, DW1469, Fiji, 19°40'S, 178°10'W, 314–377 m. Scale bar = 3 mm; scale bar for inset = 500 µm. **H.** *Bathymophila* sp. 7 of Williams *et al.* (2013). Species with turbinate shell. MNHN IM-2007-18317: EBISCO, CP2651, SE Fairway, New Caledonia, 21°29'S, 162°36'E, 883–957 m. Scale bar = 3 mm. Photo credits: H. Taylor. SEM credits: STW and DGH.

cf. *dawsoni* = *B.* sp. 12 in Williams *et al.*, 2013; Fig. 7G), but these can be separated from *Arxellia* species, because unlike *Arxellia*, they do not have beads around the rim of the umbilicus. One species, '*Bathymophila*' sp. 18 of Sumner-Rooney *et al.* (2016) has a flattened

shell with a callus, but this does not have granules of calcium carbonate on the callus.

Remarks: Two genetically and morphologically distinct clades were attributed to *Bathymophila* by Williams *et al.* (2013). The first clade

includes all the species assigned to *Bathymophila* following Marshall (1999). The second clade includes species now assigned to *Phragmomphalina* n. gen. *Bathymophila* was treated provisionally as a subgenus of *Margarites* by Quinn (1979) awaiting further evidence from radulae, but later transferred to Solariellidae by Marshall (1999) on the basis of radular morphology. The holotype of *B. euspira* (Dall, 1881) is subadult and the specimen lacks a fully developed callus. Syntypes are available for *B. euspira* var. *nitens* (Dall, 1881), which was synonymized with the nominotypical species by Quinn (1979). These syntypes are fragmented or subadult specimens, but the largest, which is broken, has a columnar callus. A single complete specimen attributed to *B. euspira* was figured in Quinn (1979; figures 1, 2, as *Margarites (Bathymophila) euspira*); this specimen has a callus over the umbilicus. Both Quinn (1979) and Marshall (1999) included other species with a callus and we concur with their concept of the genus.

Bathymophila has been characterized to date by having a heavy callus over the umbilicus (Quinn, 1979; Marshall, 1999) and obvious patches of granular deposition of calcium carbonate over the callus (Marshall, 1999). However, the clade discussed here includes several species (three sampled in molecular systematic studies and a further four for which we do not have DNA sequence data) that lack a callus, but possess instead a heavy flange around the umbilicus, which arises from a peri-umbilical ridge at the base of the columella. Only one of these species (*Bathymophila* cf. *dawsoni* = *Bathymophila* sp. 12 of Williams *et al.*, 2013) has been examined in detail. This species shows localized patches with granular deposition of calcium carbonate on the base of the columella, suggesting that this character may be particularly useful. Some of the species lacking a callus are known from only one specimen and it is possible that these specimens are damaged or immature, developing a callus later. However, the fact there are five such species known (*B. dawsoni*, *Bathymophila* cf. *dawsoni* = *B.* sp. 12 in Williams *et al.* (2013), *B. regalis*, *B. wanganellica* and *B. ziczac*) suggests that this may be the adult condition.

One further species, '*Bathymophila*' sp. 18, although provisionally identified as belonging to this genus, did not cluster with other species of *Bathymophila* in phylogenetic analyses (Sumner Rooney *et al.* 2016), despite having a shell similar in overall shape to the type species of *Bathymophila* and a callus over the umbilicus. It differs, however, in lacking calcareous granules on the callus. Further work with more taxa is needed to resolve the position of '*Bathymophila*' sp. 18 and to determine its relationships with other *Bathymophila*.

The species list for this genus is comprehensive with respect to nominal taxa, but as molecular systematic studies have shown, there are many new and undescribed species. The lack of scanning electron microscope (SEM) data for *B. micans* and its less typical shell shape make its assignment to this genus tentative.

Included species:

- Bathymophila aages* Vilvens, 2009;
- B. asphala* Marshall, 1999;
- B. bairdii* (Dall, 1889) n. comb. [*Margarites*, *Umboonium*];
- B. callomphala* (Schepman, 1908);
- **B.* cf. *callomphala* in Williams *et al.* (2013);
- B.* cf. *callomphala* in Poppe, Tagaro & Dekker (2006);
- B. dawsoni* (Marshall, 1979) n. comb. [*Archiminolia*];
- **B.* cf. *dawsoni* = *Bathymophila* sp. 12 in Williams *et al.* (2013);
- B. euspira* (Dall, 1881)** [= *B. euspira* var. *nitens* (Dall, 1881)];
- B. gravida* Marshall, 1999;
- B.* cf. *gravida* in Marshall (1999);
- ?*B. micans* (Dautzenberg & Fischer, 1896);
- ?*B. regalis* (Marshall, 1999) n. comb. [*Archiminolia*];
- B. valentia* Marshall, 1999;
- ?*B. wanganellica* (Marshall, 1999) n. comb. [*Archiminolia*];
- ?*B. ziczac* (Kuroda & Habe in Kuroda, Habe & Oyama, 1971) n. comb. [*Archiminolia*];

**Bathymophila* spp. 1, 5, 6, 7, 9, 10, 11, 15, 16, and 17 of Williams *et al.* (2013);

**Bathymophila* spp. 19 and 20 of Sumner-Rooney *et al.* (2016).

Genus *Chonospeira* new genus Herbert & Williams

(Fig. 8)

Chonospeira Herbert & Williams new genus (type species *Solariella nuda* Dall, 1896).

Clade B Williams *et al.*, 2013.

ZooBank registration: urn:lsid:zoobank.org:act:C0D6FE1E-66D0-4F4C-ADA2-6F367C5118ED

Etymology: The name refers to the very rounded whorls and funnel-like umbilicus (from the Greek *speira* (f) and *chonos* (m), respectively). Gender feminine.

Description: Shell large for the family (adult diameter > 10 mm), turbinate with rounded, shouldered whorls and strongly indented suture; umbilicus present, moderately wide and funnel-like, its margin weakly angled, somewhat nodular in subadults; peristome incomplete, columella lacking significant callus deposition. Early whorls of teleoconch generally corroded in mature specimens (Fig. 8C, D), but a juvenile specimen has sharp spiral cords and faint axial threads on first whorl (Fig. 8G, H); distinct axial ribs evident in the second and third whorls, rendering shoulder coronate; subsequent whorls for the most part smooth and glossy.

Additional observations: Eyes in the two species examined to date (*C. nuda* and *Chonospeira* sp. 3) are pigmented with an open aperture. Operculum corneous, multispiral; head-foot with extensive dark pigmentation; shells usually unpigmented. Radula lacking elongate latero-marginal plates (Fig. 8F), although small, indistinct latero-marginal plates may be evident in some radula preparations depending on tooth orientation. Shells lack colour, appearing pale grey-blue when live-collected due to presence of body; otherwise shells opaque milky-white in adults, translucent in juveniles.

Distribution: IWP, East Pacific. Depth range: Sasaki (2017) gives the range of *C. iridescens* as 60–150 m, but does not note if specimens are living; shells of *C. ostreion* (Vilvens, 2009) have been found at 420–442 m (Vilvens, 2009) and other species have been found living at 503–886 m.

Comparison: Species with a shell-shape typical of this genus, having very round, smooth whorls are sometimes found in *Bathymophila*, *Hazuregyra* (now *Minolia*), *Ilanga*, *Microgaza* and *Phragmomphalina* n. gen. *Bathymophila* can be distinguished by the presence of a callus or a peri-umbilical thickening at the base of the columella and granular deposition of calcium carbonate on the callus. *Minolia* differs by having very rounded early teleoconch whorls with heavy axial ribs. *Ilanga* and *Microgaza* shells are usually pigmented and often patterned, are usually lower-spired and do not have the combination of funnel-like umbilicus and very rounded whorls, which is characteristic of *Chonospeira* n. gen. *Phragmomphalina* n. gen. differs from *Chonospeira* n. gen. in having an umbilical septum.

Remarks: This group was recognized by Williams *et al.* (2013) as requiring a new generic assignment. The well-supported clade in that study (clade B) included only three species, none of which were identified. The first species was a juvenile from Japan (clade B, sp. 3; Fig. 8G, H) and remains unidentified. The second was a specimen from Japan originally identified as '*Microgaza*' *iridescens* (Williams *et al.*, 2008). Unfortunately, no voucher was retained, so we cannot confirm its identity. The third species (clade B, sp. 2 from Mozambique) we refer, with some reservations (see discussion below), to the type species of the genus, *Chonospeira*, *C. nuda* (Fig. 8A–F). *Chonospeira*

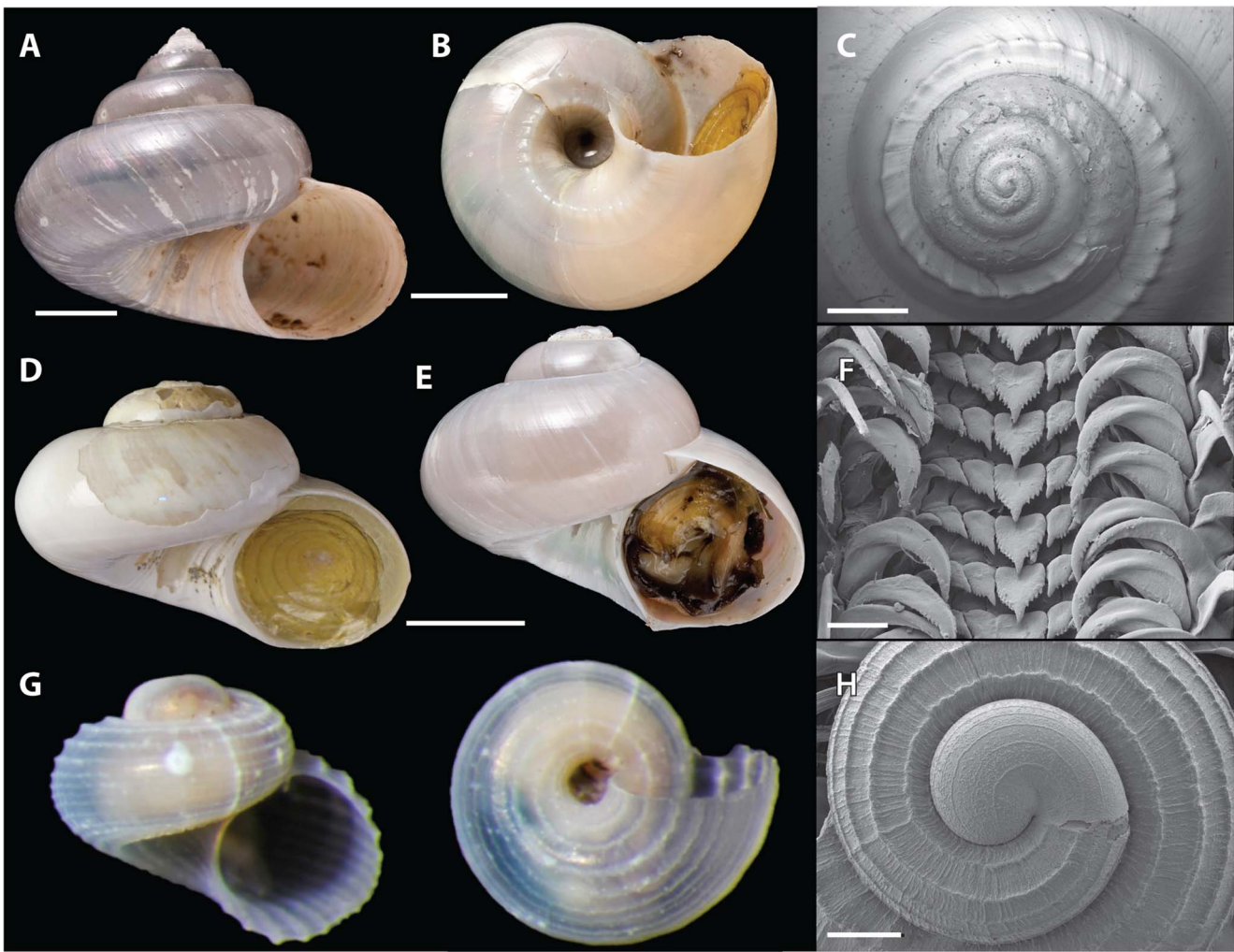


Figure 8. *Chonospeira* n. gen. (= clade B of Williams *et al.*, 2013). **A–F.** Type species of *Chonospeira* n. gen., *Chonospeira nuda* (Dall, 1896) (= clade B sp. 2 of Williams *et al.*, 2013; but see discussion in text about identification of molecular specimens). **A.** Specimen used in the study by Williams *et al.* (2013). Note high spire with early whorls intact and evidence of corrosion at tip. MNHN IM-2009-8744: MAINBAZA, CP3140, Maputo transect, Mozambique Channel, 23°33'S, 36°02'E, 886–898 m. Scale bar = 5 mm. **B.** Basal view of another specimen sequenced by Williams *et al.* (2013) showing sculpture around umbilicus. MNHN IM-2009-8739: MAINBAZA, CP3140, Maputo transect, Mozambique Channel, 23°33'S, 36°02'E, 886–898 m. Scale bar = 5 mm. **C.** SEM of spire whorls showing beaded sculpture. MNHN IM-2009-8744. Scale bar = 1 mm. **D.** Japanese specimen for which unpublished DNA sequence data are available. AORI_YK#2196: S of Daiozaki, Mie, Honshu I., Japan, 33°59'N, 136°57'E, 816 m. Shell width = 14.5 mm. **E.** US specimen for which unpublished DNA sequence data are available. SMNH 127100: Pioneer Seamount, off San Francisco, California, USA, 36°22'N 122°25'W, 999 m. Scale bar = 5 mm. **F.** Radula. Note the absence of well-developed latero-marginal plates. MNHN IM-2009-8742: MAINBAZA, CP3140, Maputo transect, Mozambique Channel, 23°33'S, 36°02'E, 886–898 m. Scale bar = 100 μ m. **G–H.** Unidentified juvenile (= Clade B sp. 3 of Williams *et al.*, 2013). AORI_YK#1407: W of Nagasaki, Kyushu I., Japan, 32°09'N, 129°31'E, 498–503 m. Shell width = 1.2 mm. **G.** Two views of shell. **H.** Protoconch and early whorls. Scale bar = 150 μ m. Photo credits: H. Taylor and YK. SEM credits: YK, DGH and STW.

nuda as we currently recognize it has an unusually wide geographic range for a solariellid, encompassing both the East Pacific temperate biogeographic zone and the tropical IWP. There is a moderate level of genetic variation amongst populations (STW & YK unpublished data) and moderate intraspecific variation in shell morphology.

The shell of specimens of clade B sp. 2 from Mozambique (Fig. 8A–C) closely resembles that of *C. nuda* from California (Fig. 8E), but the shell of the former has a higher spire, more convex whorls, the shoulder angulation is distinctly coronate on the whorls of the mid-spire and, similarly, the peri-umbilical cord has low coronations in subadults. In American *C. nuda*, these sculptural features are smooth. Some variation in basal sculpture is also evident, one specimen from Mozambique having a second basal spiral cord, albeit weak, adjacent to the peri-umbilical cord (Fig. 8B). Conchologically, Japanese specimens resemble *C. nuda* more closely in that they also lack the coronate spiral on the spire whorls and around the umbilicus. We conservatively treat all three

groups as one species, but it is possible that the Mozambique and Japanese specimens are not conspecific with *C. nuda*.

Included species:

- * *Chonospeira nuda* (Dall, 1896) n. comb. [*Solariella*];
- * *C. indescens* (Habe, 1961) n. comb. [*Ethaliopsis*, *Solariella*, *Microgaza*, *Archiminolia*];
- ? *C. ostreion* (Vilvens, 2009) n. comb. [*Archiminolia*];
- ? *C. strobilos* (Vilvens, 2009) n. comb. [*Archiminolia*];
- * *Chonospeira* sp. 1 = Clade B, sp. 3 of Williams *et al.* (2013).

Genus *Elaphriella* Vilvens & Williams, 2016

(Fig. 4B, F–H)

Elaphriella Vilvens & Williams, 2016: p. 271 (type species *Elaphriella cantharos* Vilvens & Williams, 2016; by original designation).

Clade C Williams *et al.*, 2013.

Description: Shell turbinate, with thin walls and an incomplete peristome (Fig. 4B). Columella thin, with slightly reflected edge overlapping umbilicus and small flange at base (Fig. 4F). Sculpture of first whorl of teleoconch consists of heavy spiral ribs, sometimes with thin axial threads (Fig. 4G). Umbilicus may bear thin axial threads, but no spiral cords within (Fig. 4F). For further details, see description by Vilvens & Williams (2016).

Additional observations: Of the species examined, three appear to have functional eyes with pigment and open apertures (*E. helios* and two, as yet, unnamed species), but in some deep-water species the eyes have lost pigment (*E. wareni*) or both aperture and pigment (*E. cantharos*, *E. paulinae*) (Sumner-Rooney *et al.*, 2016). Shells are unpigmented (often highly iridescent) or coloured pink or brown, and occasionally patterned. Radula lacking latero-marginal plates (Fig. 4H).

Distribution: West Pacific; living at 220–999 m (Marshall, 1999; Vilvens & Williams, 2016).

Comparison: *Elaphriella* differs from *Archiminolia* in several ways. Namely, the columella in *Archiminolia* is thicker, lacks both a reflected edge and a small flange at its base, but does have granular deposits of calcium carbonate on the columella, which *Elaphriella* does not. In *Elaphriella* there are faint, approximately vertical growth lines inside the umbilicus, whereas in *Archiminolia* there are spiral ribs. The sculpture of the first few whorls of the teleoconch in *Elaphriella* usually comprises heavy spiral ribs, often with obvious, fine axial threads; only spiral ribs are present in *Archiminolia*. Unlike *Archiminolia*, *Elaphriella* has no spiral ribs on the body whorl, although beads from earlier whorls may continue on to the body whorl.

Remarks: This genus was described by Vilvens & Williams (2016) based on the molecular systematic study of Williams *et al.* (2013), which showed a well-supported clade (clade C) comprising eight species with sequence data.

Included species:

- * ***Elaphriella cantharos*** Vilvens & Williams, 2016;
? *E. corona* (Lee & Wu, 2001) n. comb. [*Microgaza*];
- * *E. dikhonikhe* Vilvens & Williams, 2016;
- ? *E. diplax* (Marshall, 1999) n. comb. [*Archiminolia*];
- * *E. eukhonikhe* Vilvens & Williams, 2016;
- * *E. helios* Vilvens & Williams, 2016;
- * *E. leia* Vilvens & Williams, 2016;
- ? *E. meridiana* (Marshall, 1999) n. comb. [*Archiminolia*, *Spectamen*, *Zeminolia*];
- ? *E. olivaceostrigata* (Schepman, 1908) n. comb. [*Solariella*, *Archiminolia*];
- ? *E. opalina* (Shikama & Hayashi, 1977) n. comb. [*Microgaza*];
- * *E. paulinae* Vilvens & Williams, 2016;
- * *E. wareni* Vilvens & Williams, 2016;
- * *Elaphriella* spp. 5 and 6 of Williams *et al.* (2013).

Genus *Ilanga* Herbert, 1987

(Figs 1B, G, 9A, C–E)

Ilanga Herbert, 1987: p. 294 (type species *Trochus laevis* von Martens, 1881; by original designation).

Description: Shell commonly depressed turbinate to lenticular in shape, with rounded or weakly shouldered whorls; peristome briefly interrupted in parietal region; umbilicus present, frequently relatively wide (Fig. 9A). Early whorls of teleoconch sculptured only with spiral ribs, lacking strong axial sculpture, but may have fine

axial threads (Fig. 9D); later whorls often smooth, or with fine spiral ribs (rarely with spiral cords) and generally weak axial sculpture, but subsutural region sometimes with distinct pliculae. Umbilical margin ranging from evenly rounded and smooth to distinctly angular, with well-developed peri-umbilical pliculae. See Herbert (1987) for details.

Additional observations: Sixteen species have been examined to date (Williams *et al.*, 2013; Sumner-Rooney *et al.*, 2016) and all have pigmented eyes, with open apertures that appear to be functional. Radulae lack latero-marginal plates (Fig. 9E). Shells are commonly coloured and patterned (Fig. 9A).

Distribution: Southern Africa and IWP; living at 40–1,280 m (Herbert, 1987).

Comparison: This genus resembles *Microgaza* and is often confused with it. As here interpreted, *Microgaza* is known only from the Caribbean region and the Azores, whereas *Ilanga* is widely distributed in southern Africa and the IWP. These genera differ most consistently in the form of the radula: a latero-marginal plate is absent in *Ilanga*, but present in *Microgaza*. In addition, the umbilical margin of *Microgaza* has a raised spiral ridge, somewhat thickened internally with a finely granular callus deposit (compare Fig. 9C, F).

Remarks: The new species delimited to date on the basis of the molecular systematic data of Williams *et al.* (2013) and are described in Vilvens & Williams (2020).

Included species:

- Ilanga agulhasensis* (Thiele, 1925);
- I. aquamarina* (Melvill, 1909);
- I. bicarinata sphinx* Herbert, 1987;
- * *I. biradiatula* (von Martens, 1902);
- * *I. boreia* Vilvens & Williams, 2020 = *Ilanga* sp. 9 of Williams *et al.* (2013);
- * *I. comes* Vilvens & Williams, 2020 = *Ilanga* sp. 12 of Williams *et al.* (2013);
- * *I. corrineae* Vilvens & Williams, 2020 = *Ilanga* sp. 21 of Sumner-Rooney *et al.* (2016);
- I. cosmia* Vilvens & Williams, 2020;
- * *I. discus* Herbert, 1987;
- * *I. dongshaensis* Vilvens & Williams, 2020;
- I. euryomphalos* Vilvens & Williams, 2020;
- * *I. eurystoma* Vilvens & Williams, 2020 = *Ilanga* sp. 1 of Williams *et al.* (2013);
- * *I. fulgens* (Dall, 1907) = *Ilanga* sp. 4 and *Ilanga* sp. 17 of Williams *et al.* (2013);
- I. furtiva* Herbert, 1987;
- * *I. gotoi* (Poppe, Tagaro & Dekker, 2006);
- * *I. harrytaylori* Vilvens & Williams, 2020 = *I.* cf. *norfolkensis* of Williams *et al.* (2013);
- * *I. helicoides* Vilvens & Williams, 2020 = *Ilanga* sp. 20 of Williams *et al.* (2013);
- * *I. herberti* Vilvens & Williams, 2020 = *Ilanga* sp. 11 of Williams *et al.* (2013);
- I. humillima* (Thiele, 1925);
- I. impolita* Herbert, 1987;
- I. kilburni* Herbert, 1987;
- I. lauensis* Vilvens & Williams, 2019;
- * ***I. laevis*** (von Martens, 1881);
- I. livellata* Herbert, 1987;
- I. maculicincta* Herbert, 1987;
- * *I. mesebrine* Vilvens & Williams, 2020 = *Ilanga* sp. 10 of Williams *et al.* (2013);
- * *I. navakaensis* (Ladd, 1982) = *Ilanga* sp. 6 of Williams *et al.* (2013);
- I. norfolkensis* (Marshall, 1999) n. comb. [*Microgaza*];

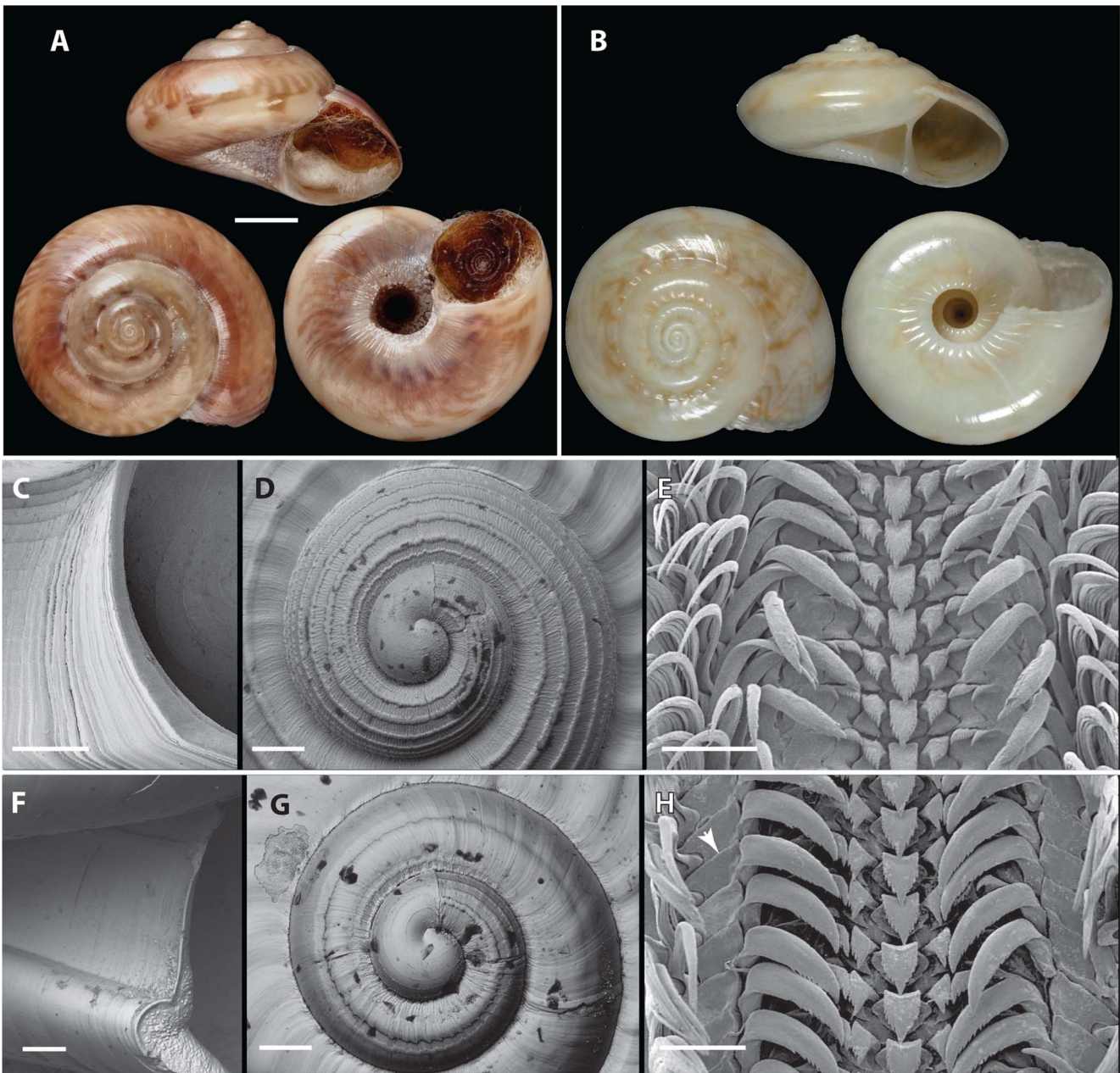


Figure 9. Comparison between *Ilanga* and *Microgaza*. **A.** Type species of *Ilanga*, *Ilanga laevisissima* (von Martens, 1881). ZMB/Moll 55 815: Cape Infanta bearing N. $\frac{1}{4}$ W. [sic.], distant 82 miles, South Africa, 57 fms (104 m). Scale bar = 3 mm. **B.** Lectotype of *Callogaza* (*Microgaza*) *rotella* Dall, 1881, type species of *Microgaza*. MCZ 7548: N of Havana, 4 miles off Morro Light, Cuba, 23°14'N, 82°25'W, 805 fms (1,472 m). Diameter = 6.5 mm. **C–E.** *Ilanga*. **C.** *Ilanga stephanophora* Vilvens & Williams, 2020. Detail of columella. MNHN IM-2014-7025: SE of New Caledonia, Banc Antigonie, Norfolk Ridge, 23°23'S, 168°02'E, 180–250 m. Scale bar = 0.5 mm. **D.** *Ilanga laevisissima*. NMSA V999: Protoconch and early whorls. SSE of Knysna, Western Cape, South Africa, 34°25'S, 23°05'E, 101 m. Scale bar = 150 μ m. **E.** *Ilanga laevisissima*. Radula. Note the absence of well-developed, elongate latero-marginal plates. NMSA V999. Scale bar = 100 μ m. **F–H.** *Microgaza rotella* (Dall, 1881). **F.** Detail of columella. MNHN IM-2013-8023: KARUBENTHOS 2012, GD33, Guadeloupe, 16°24'N, 61°33'W, 130 m. Scale bar = 200 μ m. **G.** Protoconch and early whorls. MNHN IM-2013-8023. Scale bar = 100 μ m. **H.** Radula. Note well-developed, elongate latero-marginal plates (indicated by arrows). FLMNH 264873: off Sombrero Light Key, Monroe County, Florida, USA. Scale bar = 75 μ m. Photo credits: H. Taylor. SEM credits: STW and DGH.

**I. oxeia* Vilvens & Williams, 2020 = *Ilanga* sp. 3 and *Ilanga* sp. 15 of Williams *et al.* (2013);
I. philia Vilvens & Williams, 2020;
I. platypeza Herbert, 1987;
I. polita Herbert, 1987;
I. polygramma Vilvens & Williams, 2020;
I. pykte (Vilvens, 2009) n. comb. [*Archiminolia*];
I. rhyssomphala Herbert, 1987;
**I. stephanophora* Vilvens & Williams, 2020 = *Ilanga* sp. 5 and *Ilanga* sp. 16 of Williams *et al.* (2013);

I. whitechurchi (Turton, 1932);
I. zaccaloides (Vilvens, 2009) n. comb. [*Archiminolia*];
**Ilanga* spp. 18 and 19 of Williams *et al.* (2013).

Genus *Microgaza* Dall, 1881

(Figs 1F, 5E, 9B, F–H)

Callogaza (*Microgaza*) Dall, 1881: p. 51 (type species *Callogaza* (*Microgaza*) *rotella* Dall, 1881; by monotypy).

Description: Shell lenticular, whorls weakly angled at periphery; peristome interrupted in parietal region; umbilicus wide, internally stepped (Fig. 9B). Sculpture of early whorls of teleoconch primarily spiral, axial component restricted to fine uneven growth-lines (Fig. 9G); later whorls smooth and glossy, but commonly with a coronate subsutural cord developing with growth. Umbilical margin strongly angled and demarcated by a raised ridge, with radiating peri-umbilical pliculae (Fig. 9B). Columella thin, its edge clearly delineated; internally thickened at base with granular deposition of calcium carbonate (Figs 5E, 9F). See description by Quinn (1979) for further details.

Additional observations: Eyes are pigmented with open apertures. Shells are nacreous, sometimes appearing to be white, and may have yellow-brown patterns. Radula with well-developed latero-marginal plates (Fig. 9H).

Distribution: Caribbean and the Azores. Quinn gives a 'possible' depth range for this genus as 46–1,472 m, but says they most commonly occur between 100 and 200 m. The living specimens used by Sumner-Rooney *et al.* (2016) were collected from depths of 85–130 m. A single living specimen used in that study was reportedly found at 1 m (MNHN IM-2013-20336), but this is almost certainly in error.

Comparison: See description of *Ilanga*.

Remarks: Although not sampled by Williams *et al.* (2013), DNA sequences included in Sumner-Rooney *et al.* (2016) confirm that this genus is distinct from *Ilanga*. Quinn (1979) recognized only three taxa for *Microgaza*, including two subspecies of *M. rotella*. He distinguished *M. r. inornata* Quinn, 1979 and *M. r. rotella* (Dall, 1881) by the presence of beads on the shell whorls in the latter (absent in the former) and by their geographic distribution. He suggested the two subspecies were geographically isolated from each other, with the ranges of *M. r. rotella* (southeastern Gulf of Mexico, the Straits of Florida, occasionally as far north as Key Largo, Cuba and south through the Antillean arc) and *M. r. inornata* (from Cape Hatteras, North Carolina to Miami, Florida) separated by a transitional zone, where intermediate forms might be found. By this definition, specimens from Guadeloupe should all be *M. r. rotella*. However, forms with and without beads on the shell (apparently corresponding to *M. r. rotella* and *M. r. inornata*, respectively) have been collected on MNHN expeditions to this locality. As shown in the Sumner-Rooney *et al.*'s (2016) phylogeny, sequences from these different forms are genetically identical and specimens from the northern range of the genus are needed to confirm the possible synonymy of the two subspecies. The third species, *M. vetula* Woodring, 1928, which was originally described from a fossil and was recognized in Recent samples by Quinn (1979), has not been included in molecular systematic studies because no suitable samples were available.

Included species:

* *Microgaza rotella* (Dall, 1881);

M. vetula Woodring, 1928.

Genus *Minolia* A. Adams, 1860

(Fig. 10)

Minolia A. Adams, 1860: p. 336 (type species: *Minolia punctata* A. Adams, 1860, by monotypy).

Hazuregyra Shikama, 1962: p. 41 (type species *Hazuregyra watanabei* Shikama, 1962; by monotypy).

Description: Shell usually taller than wide, sometimes turbanate, but whorls usually somewhat flat-sided; peristome complete or almost complete (Fig. 10A, B). Spiral ribs within umbilicus, sometimes

beaded (Fig. 10E). Sculpture of early teleoconch includes heavy axial ribs and very rounded whorls (Fig. 10C, F), occasionally with microscopic spiral threads in the intervals.

Additional observations: All *Minolia* species used in the molecular phylogenetic studies have pigmented eyes with open apertures (Williams *et al.*, 2013; Sumner-Rooney *et al.*, 2016). Shells may be unpigmented or have pink-brown patterns. Radula with small, trigonal latero-marginal plates, retaining a filament-like shaft and cusp (Fig. 10D, G). Latero-marginal plates are small and may be difficult to observe in some preparations.

Distribution: Japan, Taiwan and northeastern Pacific. Only Japanese specimens were used in the molecular systematic studies; distribution of this genus in Taiwan and northeastern Pacific is inferred by the presence of species with shell morphology fitting the generic identity. Living specimens found at 50–900 m (Hasegawa, 2009; Williams *et al.*, 2013), with most species being found at 50–350 m (Sasaki, 2017) and only *Minolia watanabei* occurring in much deeper water (210–900 m; Hasegawa, 2009).

Comparison: Shells very similar to *Spectamen* and *Solariella*, but *Minolia* species have only well-developed axial ribs on strongly rounded early whorls and spiral sculpture is much weaker (at most, only spiral threads are present) or absent (compare Fig. 10C, F with Figs 3D, 11D, 11F).

Remarks: The currently recognized type material for *Minolia punctata* comprises four shells in the collections of the NHMUK (NHMUK 1878.10.16.6; Fig. 10A) and have the note 'Probably types' on an accompanying label. While this supports our view that the four shells are type specimens, two comments in the NHMUK Mollusca register suggest otherwise. These are: 'Collected in Japanese & Korean seas by Capt. H. C. St John R. N. of HMS Sylvia' and alongside it, 'Presented by Dr J. Gwyn Jeffreys'. Both comments refer to several lots of which NHMUK 1878.10.16.6 is just one.

According to several websites (e.g. <http://www.pdavis.nl/ShowBiog.php?id=1680>; <http://www.thornburyroots.co.uk/families/st-john-henry-c/>), HMS Sylvia was launched on 20 March 1866 and between 1869 and 1877 was commanded by Henry Craven St John. St John was a Lieutenant in 1857, promoted to Commander in 1866 and to Captain in 1873. These events all postdate Adams' description in 1860, which would suggest that the lot registered as NHMUK 1878.10.16.6 cannot be the one that Adams examined. However, Kathie Way, the previous Collections Manager for Mollusca at the NHMUK, who had an expert knowledge of handwriting in the collection, suggested the writing on the label was in a different hand to the comments in the register and that the note on the label may have been added later and/or in error. Alternatively, Adams' samples may have been mixed with Jeffreys' at some point.

If we accept the current type status as correct, then *Minolia subangulata* Kuroda & Habe, 1952 is a junior synonym of *Minolia punctata* (new synonymy) and the species usually referred to as '*punctata*' (e.g. Sasaki, 2017: pl. 26, fig. 13) is actually *Minolia pseudobscura* (Yokoyama, 1927), the original description of which was based on a Pleistocene fossil. The species referred to as *Minolia* sp. in Williams *et al.* (2013) is now thought to be *Minolia pseudobscura*.

Williams *et al.* (2013) suggested that *Hazuregyra* Shikama, 1962 might be synonymized with *Minolia* on the basis of molecular systematic data, which showed that *Minolia* and *Hazuregyra* were genetically similar and were consistently shown to be sister taxa. In this study, we formalize that suggestion and relegate *Hazuregyra* to the synonymy of *Minolia*.

All specimens of *Minolia* sequenced to date are Japanese, but *Minolia gemmulata* Kuroda & Habe, 1971 and *Minolia peramabilis* (Carpenter, 1864) are undoubtedly members of this genus (Herbert, 1987; Hickman & McLean, 1990), and this extends the geographic range of the genus to include Taiwan and the northeast Pacific, respectively. The description of '*Solariella*' *shimajiriensis* MacNeil,

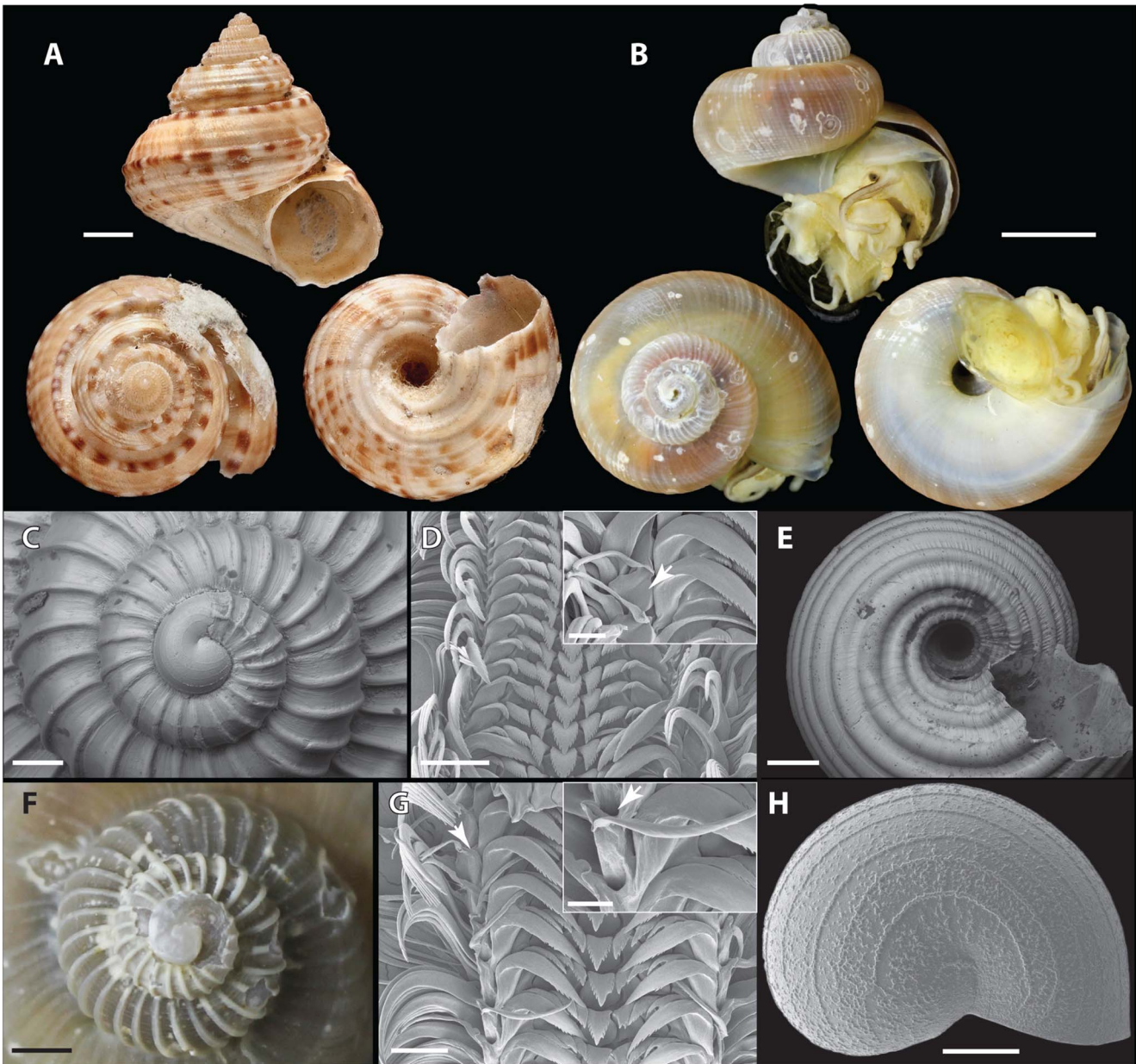


Figure 10. *Minolia* species. **A.** Probable syntype of *Minolia punctata* A. Adams, 1860, type species of *Minolia*. NHMUK 1878.10.16.6: Mino Sima, Japan, 30°19'N, 129°7'E, 50 fms (91 m). Scale bar = 2 mm. **B.** Type species of *Hazuregyra*, *Minolia watanabei* (Shikama, 1962). Specimen used in Williams *et al.*'s (2013) study as *Hazuregyra watanabei*. AORI_YK#1464. Scale bar = 2 mm. **C–E.** *Minolia punctata*. **C.** Protoconch and early whorls. NHMUK 1878.10.16.6. Scale bar = 150 μ m. **D.** Radula. Detail in inset. Note the presence of small trigonal latero-marginal plates, retaining a filament-like shaft and cusp (indicated by arrow in inset). The plates are not visible in the larger image. AORI (no registration number): off Anori, Mie, Honshu I., Japan, 34°20'N, 136°55'E, 80 m. Scale bar = 100 μ m (20 μ m in inset). **E.** Base of shell. NHMUK 1878.10.16.6. Scale bar = 1 mm. **F–H.** *Minolia watanabei*. **F.** Early whorls. NSMT-Mo 92574: off Kinkazan, Miyagi, Honshu I., Japan, 37°59'N, 141°49'E, 253–259 m. Scale bar = 0.5 mm. **G.** Radula. Note the presence of trigonal latero-marginal plates, retaining a filament-like shaft and cusp (indicated by arrow). Detail in inset. NSMT-Mo 92574. Scale bar = 50 μ m (20 μ m in inset). **H.** Protoconch of encapsulated embryo taken from adult umbilicus. NSMT-Mo 92573: off Kesenuma, Miyagi, Honshu I., Japan, 38°39'N, 142°02'E, 373–375 m. Scale bar = 100 μ m. Photo credits: H. Taylor and YK. SEM credits: STW and YK.

1960 was based on a Pleistocene fossil, but this is most likely conspecific with *Minolia gemmulata* (syn. nov.).

This genus is often confused with umboniine genera, especially *Monilea* Swainson, 1840.

Included species:

- **Minolia nysson* (Dall, 1919);
- ?*M. peramabilis* (Carpenter, 1864);
- **M. pseudobscura* (Yokoyama, 1927) (= *M. sp.* in Williams *et al.*, 2013);
- * ***M. punctata* A. Adams, 1860;**
- ?*M. shimajiriensis* (MacNeil, 1960) n. comb. [*Solariella*];

**M. watanabei* Shikama, 1962 n. comb. [*Hazuregyra*]. Hasegawa (2009) noted that this species includes many different forms that may prove to be different species.

Genus *Phragmomphalina* new genus Herbert & Williams

(Figs 5D, 7A–F)

Phragmomphalina Herbert & Williams (type species *Phragmomphalina vilvensis* Herbert & Williams, n. sp., see below).

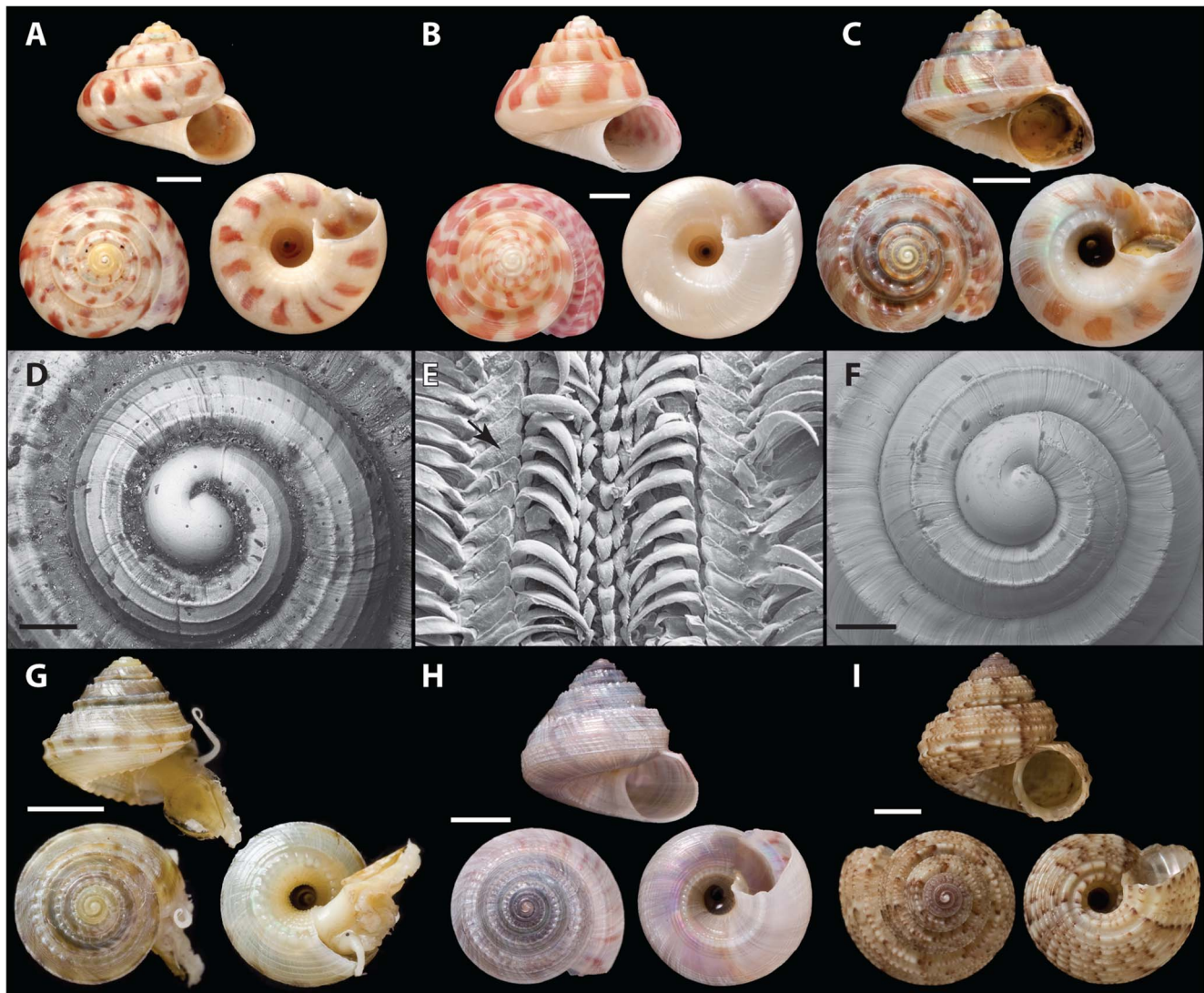


Figure 11. *Spectamen* species. **A.** Holotype of *Trochus philippensis* Watson, 1881, type species of *Spectamen*. NHMUK 1887.2.9.290: Challenger Expedition, stn 161.1.4.1874, off the entrance to Port Philipp, Australia, 38°22.5'S, 144°36.5'E, 33 fms (60 m). Scale bar = 2 mm. **B.** Syntype of *Minolia bellula* Angas, 1869. Note absence of colour on shell base. NHMUK 1870.10.26.147: Brisbane Water, New South Wales, Australia. Scale bar = 2 mm. **C.** *Spectamen bellulum* used in study by Williams *et al.* (2013); (as *S. philippense*). Note shell has half a whorl less than the type specimen figured and still has colour patches on the base of the last whorl. NHMUK 20110452: N Moreton I., Moreton Bay, Queensland, 26°56.60'S, 153°24.25'E, 31 m. Scale bar = 2 mm. **D.** *Spectamen philippense*. Protoconch and early whorls. NHMUK 1887.2.9.290. Scale bar = 150 μ m. **E.** *Spectamen philippense*. Radula. Note well-developed, elongate latero-marginal plates (indicated by arrow). NMSA K3169: Twofold Bay, New South Wales, Australia, 9–37 m. **F.** *Spectamen bellulum*. Protoconch and early whorls. NHMUK 20110452. Scale bar = 150 μ m. **G, H.** *Spectamen* species used in molecular systematic studies. **G.** *Spectamen* sp. 1 from Williams *et al.* (2013). Note pigmented eye. MNHN IM-2007-18 351: PANGLAO2004, T39. W Pamilacan I., Cervera Shoal, Philippines, 100–138 m. Scale bar = 2 mm. **H.** *Spectamen* sp. 4 from Williams *et al.* (2013). WAM S25789: off Bald I., Western Australia, between 35°16.11–35°17.17'S and 118°43.12–118°42.36'E, 973–999 m. Scale bar = 2 mm. **I.** Example of South African radiation. Holotype of *Spectamen geruloides* Herbert, 1987. NMSA B3473/T3432: off Scottburgh, KwaZulu-Natal, South Africa, 100 m. Scale bar = 2 mm. Photo credits: H. Taylor. SEM credits: STW and DGH.

Bathymophila Williams *et al.*, 2013; Sumner-Rooney *et al.*, 2016 (both in part).

ZooBank registration: urn:lsid:zoobank.org:act:5846028B-3587-4E0F-AC84-414D75FC3A2D

Etymology: From Greek *phragmos* [φραγμός] (n), a fence, barrier or dividing structure and *omphalos* [ομφαλός] (m), a navel; refers to septum-bearing umbilicus. Gender feminine.

Description: Shell large for the family (adult diameter > 10 mm), depressed turbinate to trochoidal-turbinate, whorls usually rounded at periphery and whorls of spire moderately convex or somewhat flat-sided, suture shallowly to moderately indented;

umbilicus present, of moderate width, usually covered over by thin septum in larger specimens; base with 3–5 peri-umbilical spiral cords rendered nodular by radiating plicae; granular deposition of callus restricted more or less to columella and does not occur on septum (Figs 5D, 7C). Shell smooth, glossy and slippery; early whorls of teleoconch sculptured only with low spiral cords (Fig. 7D); axial sculpture weak until start of third whorl, thereafter whorls weakly shouldered and with 1 or 2 strong subsutural spiral cords rendered nodular by short subsutural axial pliculae; sculpture weak or obsolete on last adult whorl. Protoconch with 5–8 spiral threads.

Additional observations: Eyes pigmented in *Phragmomphalina* spp. 1, 2 and 3 and *P. diadema*, but aperture lacking in all but *Phragmomphalina*

sp. 3, giving the impression that the eyes of most species have withdrawn into the eyestalks (Williams *et al.*, 2013; Sumner-Rooney *et al.*, 2016). Shell pigmentation weak, early whorls translucent white, apical surface of later whorls commonly pale pinkish with occasional axial bands of a slightly darker shade; base uniformly white. Radula with moderately elongate latero-marginal plates lacking a filament-like shaft and cusp (Fig. 7E).

Distribution: IWP, East Pacific; living at 430–883 m (Marshall, 1999; Williams *et al.*, 2013).

Comparison: Similar to *Elaphriella*, *Archiminolia* and *Bathymophila*. Both *Elaphriella* and *Archiminolia* differ from the new genus in lacking an umbilical septum. Furthermore, in *Archiminolia* the peri-umbilical sculpture is much weaker (i.e. unlike *Phragmomphalina* n. gen., *Archiminolia* lacks strong spiral cords cut by radiating pliculae). *Bathymophila* differs from *Phragmomphalina* n. gen. in having the umbilicus occluded by a thick granular deposit on the callus rather than a thin septum. In the latter, the granular deposition of the callus is less extensive and is restricted to the columella pillar and nearby area (compare Fig. 5B, D); the septum, in *Phragmomphalina* n. gen. though lustreless, is not as strongly granular (Figs 5D, 7C) as the callus in *Bathymophila* (Fig. 5B).

Remarks: Based on molecular systematic data, the species here assigned to *Phragmomphalina* n. gen. were considered part of a broadly reinterpreted concept of *Bathymophila* (Williams *et al.*, 2013; Sumner-Rooney *et al.*, 2016), within which they formed one of two well-supported subclades. Further investigation from a morphological perspective has revealed additional anatomical characters that consistently differ between the members of the *Phragmomphalina* n. gen. subclade and the other subclade, which is thought to contain species of *Bathymophila* s.s. We consider these differences sufficient to warrant recognition at the generic level and the relevant shell characters are detailed in the comparison above. Anatomical differences relate to the gross morphology of the eyes (pigmented in *Phragmomphalina* n. gen. and apparently unpigmented in a gross examination of *Bathymophila*) and the latero-marginal plate of the radula, which in *Bathymophila* is less elongate and retains a filament-like shaft and cusp extending from its antero-medial corner.

Included species:

- * *Phragmomphalina alabida* (Marshall, 1979) n. comb. [*Solariella* (*Microgaza*), *Archiminolia*];
- * *P. diadema* (Marshall, 1999) n. comb. [*Archiminolia*];
- * *P. tenuiseptum* (Marshall, 1999) n. comb. [*Archiminolia*];
- * ***P. vilvensi* Herbert & Williams n. sp.** (= *Bathymophila* sp. 4 from Williams *et al.* (2013);
- * *Phragmomphalina* species 1 (= *Bathymophila* sp. 2 of Williams *et al.*, 2013);
- * *Phragmomphalina* species 2 (= *Bathymophila* sp. 14 of Williams *et al.*, 2013);
- * *Phragmomphalina* species 3 (= *Bathymophila* sp. 21 of Sumner-Rooney *et al.*, 2013).

***Phragmomphalina vilvensi* new species**
Herbert & Williams

Fig. 7A, D-F

Bathymophila sp. 4 Williams *et al.*, 2013.

ZooBank registration: urn:lsid:zoobank.org:act:A9FFE7F9-AEB0-4B04-AABC-8C0BA3AB696A

Type material: Holotype (Fig. 7A), northern Mozambique Channel, east of Leven Bank, off NW Madagascar, MIRIKY Stn CP3192, 12°26'S, 48°13'E, 580 m, MNHN IM-2009-8769).

Seven paratypes 1–7: northern Mozambique Channel, east of Leven Bank, off NW Madagascar, MIRIKY: paratype 1: stn

CP3192, 12°26'S, 48°13'E, 580 m (MNHN IM-2009-8771); paratype 2: stn CP3186, 12°34'S, 48°09'E, 625 m (MNHN IM-2009-8770); paratypes 3–7: stn CP3221, 12°47'S, 48°08'E, 782 m (MNHN IM-2009-8762, MNHN IM-2009-8763, MNHN IM-2009-8764, MNHN IM-2009-8772, MNHN IM-2009-8773).

Etymology: Named for Claude Vilvens of Oupeye, Belgium, who is a Scientific Associate of MNHN, in recognition of his important work on the taxonomy of solariellid gastropods.

Description: Shell moderately large (maximum diameter 15.0 mm), broadly conispiral; whorls rather flat-sided, suture shallowly indented; spire prominent (length/diameter = 0.71–0.77); early whorls of spire shouldered, with rounded periphery, later whorls usually (but not always) with slight, though distinct angulation just above abapical suture; start of last adult whorl sometimes with a second, even weaker angulation at or just below periphery; angulations obsolete on latter half of last adult whorl; sculpture weak, shell essentially smooth and glossy, but bearing distinct coronations at shoulder angulation and beaded radial plicae around umbilical rim; base slightly flattened, umbilicus in adults closed by a thin septum (commonly broken); teleoconch of up to 5.5 whorls. First whorl of teleoconch with 5 or 6 low, spiral ribs (Fig. 7D), increasing to 8–10 on third whorl through intercalation, uppermost spiral rib forms weak shoulder; axial sculpture on these early whorls indistinct, but shoulder spiral becoming stronger and, due to development of short subsutural pliculae, more coronate on third whorl; spiral lirae below shoulder evanesce during fourth whorl, but shoulder develops into a rounded and coronate subsutural cord that divides into 2 close-set coronate cords (the lower one weaker) towards end of third whorl; cords usually persist during subsequent whorls, but become weaker and less strongly coronate near outer lip, evanescing completely in some specimens; remainder of last adult whorl smooth and glossy, sculptured only by fine, collabral growth lines, outer layers of the shell are somewhat transparent and faint spiral pattern of underlying nacre visible; base for the most part similarly smooth and glossy, but medial third with 3–7 spiral cords bordering umbilicus (cords strongest in juveniles); cords rendered nodular by about 25 coarse pliculae radiating from umbilical margin. Umbilical margin a strongly thickened, rounded cord; umbilicus patent, usually covered over by a thin septum, but still remaining as a shallow concavity; septum lacking in juveniles and even some shells of near adult size, the remaining umbilicus relatively narrow and steep-sided (Fig. 7F). Aperture subquadrate to obliquely D-shaped; peristome interrupted in parietal region; columella almost straight, somewhat thickened apically and covered with a lustreless, granular callus deposit; callus spreading as a thin septum over umbilicus; septum not obviously granular, but lustreless and often with distinct lines of growth; junction of columella and basal lip rendered angular by peri-umbilical cord, sometimes with a boss-like nodule at its end; outer lip thin and simple; interior nacreous, lacking labral ornamentation. Protoconch (Fig. 7D) of *c.* 1.25 whorls (diameter *c.* 330 µm), translucent milky-white; lacking apical beak; sculptured with fine, widely spaced spiral threads; terminal lip straight, not thickened. Colour of whorls of spire translucent milky-white, with faint pink/green iridescence; later whorls commonly with a distinct pale pink wash, usually with collabral variation in intensity; base translucent silvery-white; peri-umbilical cord opaque white, with nacreous interior. Dimensions: holotype (largest specimen), length 11.0 mm, diameter 15.0 mm. Operculum corneous, pale straw-brown, multispiral with short growing edge.

Radula (Fig. 7E) that of a typical solariellid, comprising *c.* 30 transverse rows of teeth; cusps of rachidian and inner three pairs of lateral teeth with relatively fine denticles, lacking a clearly dominant medial denticle; a well-developed elongate latero-marginal plate present.

Distribution: Known only from the northern Mozambique Channel, east of Leven Bank, off NW Madagascar; living at 580–782 m.

Remarks: In terms of its size, distinct subsutural sculpture and strong peri-umbilical spiral cords and axial plicae, *P. vilvensi* n. sp. resembles only *P. diadema* from the southwestern Pacific (Fig. 7B). In the latter species, however, the axial sculpture on the spire is stronger and the spiral lirae often continue on to the start of the last adult whorl. Additionally, in *P. vilvensi* the coronate subsutural cord is usually duplex on the later whorls, the whorls of the spire are less convex and the base more flattened, giving the shell a somewhat biconic profile compared to the subglobose profile of *P. diadema*. In both *P. tenuiseptum* and *P. alabida* the whorls are more convex than in *P. vilvensi* and, in addition, the subsutural and peri-umbilical sculpture is weaker.

Genus *Spectamen* Iredale, 1924

(Figs 1D, E, 11)

Spectamen Iredale, 1924: p. 227 (type species *Trochus philippensis* Watson, 1880; by original designation).

Zemolinia Finlay, 1926: p. 371 (type species *Minolia plicatula* Murdoch & Suter, 1906; by original designation; this synonymy has not yet been tested by molecular systematic data).

Minolops Iredale, 1929: p. 169 (type species *Minolia emendata* Iredale, 1924; by original designation; this synonymy has not yet been tested by molecular systematic data).

Description: Shell low to high turbinate; whorls rounded or flat-sided, often with a tabulate shoulder; peristome complete or nearly so; umbilicus present, moderate to wide (Fig. 11A–C, G–I). First whorl of teleoconch sculptured only by spiral ridges (Fig. 11D, 1F); axial sculpture, if present, develops subsequently, usually in the form of subsutural pliculae that render shoulder region crenulate or coronate; later whorls commonly with spiral lirae or cords, sometimes with close-set axial pliculae in their intervals. Base ranging from smooth to strongly corded; umbilical margin evenly rounded to distinctly angled, with a nodular peri-umbilical cord; internal sculpture of umbilicus similar to that on base.

Additional observations: All four *Spectamen* species used in the molecular systematic studies have pigmented eyes with open apertures (Williams *et al.*, 2013; Sumner-Rooney *et al.*, 2016). Shells may be unpigmented or have pink-brown or yellow-brown patterns. Radula with well-developed, elongate latero-marginal plates (Fig. 11E).

Distribution: West Pacific (source of sequenced material); living at 31–973 m (Williams *et al.*, 2013). On the basis of morphology, additional species from southern Africa are currently considered to belong to this genus (Herbert, 1987), but their relationship to taxa from the West Pacific requires further molecular systematic study.

Comparison: Shells are very similar to *Solariella* and *Minolia*, but the three genera are reciprocally monophyletic, with *Spectamen* shown to be sister to *Solariella* in molecular systematic studies (Williams *et al.*, 2013). *Spectamen* species are sculptured only with strong spiral cords on the early teleoconch whorls; the axial ribs present in *Solariella* and *Minolia* (Fig. 11A, F) are lacking.

Remarks: Species included in the molecular systematic studies all have conical, rather than turbinatate shells; the generic assignment of species with turbinatate shells or rounded whorls has not been tested. South African species assigned to *Spectamen* by Herbert (1987) may belong to a separate radiation that is distinct from *Spectamen* s.s. This radiation shares some characters with *Spectamen* s.s. (presence of latero-marginal plates, early whorls of teleoconch with spiral cords and absence of axial ribs), but species show considerably more variation in shell shape and sculpture than the specimens examined in the molecular systematic studies. Species assigned to an Australian/New Zealand radiation tend to have lower-spined

shells with round whorls and may represent yet a third radiation. Further work is needed to confirm the status of these groups. See Herbert (1987) for further details about South African species and Marshall (1999) for details about most of the Australian/New Zealand species (some assigned to *Solariella* in that paper).

Williams *et al.*'s (2013) study included material that was provisionally identified as the type species, *S. philippense*. However, further morphological examination of this material (Fig. 11C) and comparison with the holotype of *S. philippense* (NHMUK 1887.2.9.290; Fig. 11A) and two syntypes of *S. bellulum* (Angas, 1869) (NHMUK 1870.10.26.147; Fig. 11B) suggests that the sequenced specimens are subadult specimens of *S. bellulum* (whorl-for-whorl the sequenced specimens are half a whorl smaller than the type specimens). The sequenced specimens exhibit colour patterns on the base of the last whorl, whereas the types of *S. bellulum* do not. However, until further data are available, we take the conservative view that these differences reflect intraspecific variation.

Included species *Spectamen* s.s.:

**Spectamen bellulum* (Angas, 1869);

?*S. euteium* (Vilvens, 2009) n. comb. [*Solariella*];

**S. laevior* (Schepman, 1908);

**S. mutabile* (Schepman, 1908);

***S. philippense* (R. B. Watson, 1880);**

**Spectamen* spp. 1, 2 and 4 of Williams *et al.* (2013).

Species included in South African radiation of Spectamen (DNA sequence data not available):

Spectamen adarticulatum (Barnard, 1963);

S. flavum Herbert, 1987;

S. franciscanum (Barnard, 1963);

S. gerula Herbert, 1987;

S. geruloides Herbert, 1987;

S. martensi Herbert, 2015;

S. multistriatum (Thiele, 1925);

S. pardalis Herbert, 1987;

S. roseapicale Herbert, 1987;

S. rubiolae Herbert, 1987;

S. ruthae Herbert, 1987;

S. sulculiferum Herbert, 1987.

Species included in Australian/New Zealand radiation of Spectamen (DNA sequence data not available):

Spectamen basilicum (Marshall, 1999) n. comb. [*Solariella*];

S. exiguum (Marshall, 1999) n. comb. [*Solariella*];

S. flavidum (Marshall, 1999) n. comb. [*Solariella*];

S. luteolum (Powell, 1937);

S. plicatulum (Murdoch & Suter, 1906);

S. semireticulatum (Suter, 1908);

S. tryphenense (Powell, 1930);

S. verum (Powell, 1937).

Genus *Suavotrochus* Dall, 1924

(Fig. 12A–D)

Suavotrochus Dall, 1924: p. 90 (type species *Solariella lubrica* Dall, 1881; by monotypy).

Description: Spire elevated, somewhat tumid, distinctly cyrtconoid; subsutural region with strong coronations on later whorls (Fig. 12A); umbilical margin strongly plicate (Fig. 12B). Early teleoconch with one spiral rib that develops into shoulder cord (Fig. 12C). Protoconch with seven spiral threads. See Quinn (1979) for further details.

Additional observations: *Suavotrochus lubricus* has pigmented eyes with open apertures. Shells are unpigmented and often pearly iridescent. Radula lacking elongate latero-marginal plates (Fig. 12D).

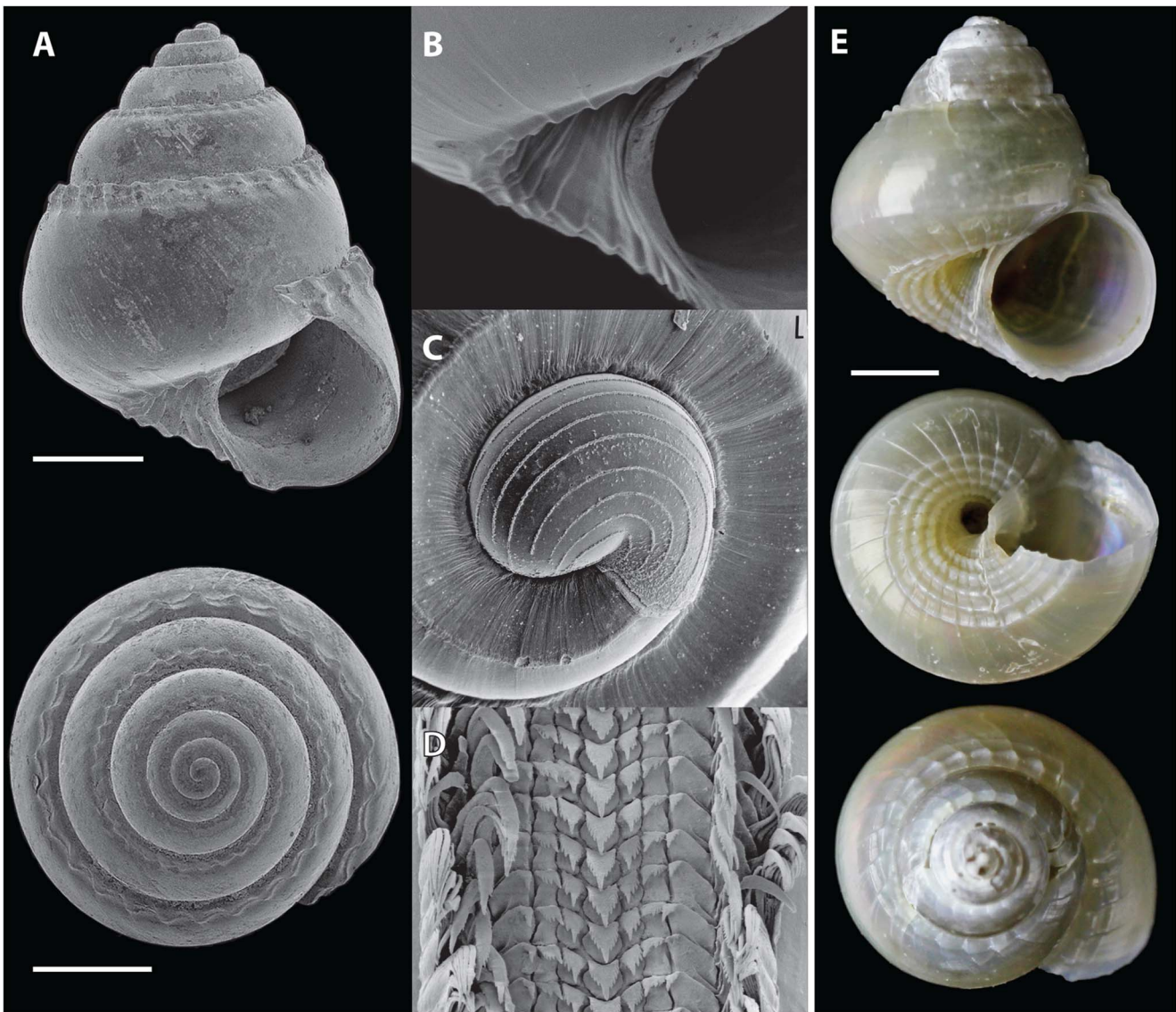


Figure 12. Comparison between *Suavotrochus* and '*Suavotrochus*' sp. (sequenced in study by Williams *et al.*, 2013). **A–D.** Type species of *Suavotrochus*, *Suavotrochus lubricus* (Dall, 1881). **A.** Lectotype of *Margarita lubrica* Dall, 1881. Two views of shell. USNM 95061: 2.4 miles NW of Morro Castle, Havana, Cuba, Straits of Florida, 23°13'59.88"N, 82°25'0.12"W, 1472 m. Scale bars = 1 mm. **B.** Columella detail. MNHN (no registration number): BRESIL, CB106. N.O. Marion Dufresne, cruise 55, southeast Brazil, 23°54'S, 42°10'W, 830 m. **C.** Protoconch. MNHN (no registration number): Gulf of Mexico, off Louisiana, 28°03'N, 90°15'W, 356 m, coll. Pequegnat. **D.** Radula. Note the absence of well-developed latero-marginal plates. MNHN (no registration number): BRESIL, CB106. N.O. Marion Dufresne, cruise 55, off southeast Brazil, 23°54'S, 42°10'W, 830 m. **E.** '*Suavotrochus*' sp. Specimen used in Williams *et al.*'s (2013) study. AORI_YK#1382: W of Amami I., Japan, 28°36'N, 127°04'E, 704–730 m. Scale bar = 1 mm. Photo credits: YK. SEM credits: G. Harasewych, AW and YK.

Distribution: Caribbean. Depth: 73–1,472 m (Rosenberg *et al.*, 2009), but Quinn (1979) notes that *S. lubricus* probably inhabits depths of 200–500 m, a suggestion supported by additional samples examined by Cavallari *et al.* (2019).

Comparison: This monotypic genus is easily distinguished from other genera in this review by its distinctive shell characters and overall shell shape.

Remarks: Quinn (1979) recognized only *S. lubricus* in this genus. New, unpublished molecular data suggest that the Japanese specimen, which was tentatively referred to *Suavotrochus* and sequenced by Williams *et al.* (2013) (Fig. 12E), is not congeneric with the type species, despite strong similarities in gross shell shape. Further investigation is needed.

Included species:

* *Suavotrochus lubricus* (Dall, 1881).

Genus *Zetela* Finlay, 1926

(Fig. 13)

Zetela Finlay, 1926: p. 359 (type species *Mimolia textilis* Murdoch & Suter, 1906; by original designation).

?*Lamellitrochus* Quinn, 1991: p. 81 (type species *Margarita lamellosa* Verrill & Smith, 1880; by original designation; molecular confirmation of this synonymy is not yet available).

Description: Shell trochiform to turbinate; whorls rounded or somewhat flat-sided, often shouldered; base rounded, with moderately

wide umbilicus; peristome briefly interrupted in parietal region (Fig. 13A–C). Early teleoconch whorls with both spiral ridges and axial ribs, producing a reticulate sculpture; intersection of ridges and ribs often nodular, sometimes sharply so (Fig. 13D, G); basal sculpture similar, but generally weaker; umbilical margin evenly rounded to angular with a nodular peri-umbilical cord (Fig. 13E, H); internal sculpture of umbilicus similar to that on base. See Marshall (1999) for further details.

Additional observations: The three *Zetela* species included in the molecular phylogeny (*Zetela* spp. 1–3) have pigmented eyes and where known (*Zetela* spp. 2, 3), the eyes have an open aperture (Williams *et al.*, 2013; Sumner-Rooney *et al.*, 2016). Modelling by Sumner-Rooney *et al.* (2016) revealed a dent-like disfigurement in the shape of both eyes of one species (Williams *et al.*, 2013; *Zetela* sp. 1), which was also seen to a lesser extent in other congeneric taxa examined by Sumner-Rooney *et al.* (2016). Shells are unpigmented; they may be iridescent but species from colder waters are often chalky in appearance. Several species examined in this group have very thick tentacles and darkly pigmented tissue. Radula lack latero-marginal plates, but the tooth that gives rise to the latero-marginal plates sometimes has a reduced shaft and cusp (Marshall, 1999) (Fig. 13F).

Distribution: Indian, Pacific and Southern Oceans. Depth: *Zetela* (three species included in molecular systematic studies) found living at 272–1,145 m; *Lamellitrochus* at 25–2,350 m (Quinn, 1991; Rosenberg *et al.*, 2009).

Comparison: The prickly spiral cords typical of many *Zetela* species are not found in other solariellid genera, except the Caribbean genus *Lamellitrochus*, which is considered a junior synonym of *Zetela* by Marshall (1999). *Zetela* may be superficially similar to some seguenzioid genera (e.g. *Calliotropis*), but the latter have a brown, olive or yellow periostracal layer, giving the shell surface a lustreless appearance (Hickman & McLean, 1990). Some *Zetela* species may also resemble South African taxa currently referred to *Spectamen* (Herbert, 1987) but, in *Spectamen* the radula has well-developed latero-marginal plates (not the case for *Zetela*). Less prickly specimens of *Zetela* may perhaps be mistaken for *Minolia*, but in *Zetela* the early whorls of the shell are not as conspicuously rounded and the early whorls of the teleoconch have spiral cords in addition to axial ribs.

Remarks: All *Zetela* specimens for which molecular sequence data are available, have the shell characteristics outlined above (where known); this is also true for the type species, for which DNA sequence data are lacking. Although radular characters are variable amongst species currently accepted as belonging to *Zetela*, all species examined lack well-developed latero-marginal plates. Some, however, have rudimentary latero-marginal structures.

Other species currently assigned to *Zetela*, for which we do not have molecular data, show a range of character states for shell sculpture, suggesting that some may be incorrectly assigned. For instance, *Z. turbynei* (Barnard, 1963) and *Z. semisculpta* (von Martens, 1904) from southern Africa lack axial ribs on early teleoconch whorls (Herbert, 1987, 2015) and may not belong in this genus. Although '*Zetela*' *alphonsi* Vilvens, 2002 was treated as belonging to *Zetela* by Sumner-Rooney *et al.* (2016), anatomical characters, and specifically the presence of a latero-marginal plate, suggest it may not belong to this genus (Schwabe *et al.*, 2017). The eye morphology of '*Z.*' *alphonsi* also differs from other *Zetela* species examined; '*Z.*' *alphonsi* has an unpigmented eye lacking an aperture (Sumner-Rooney *et al.*, 2016).

Some South African and Antarctic taxa have both rudimentary latero-marginal structures and a wide, flat, reflected columella. It is possible that these may belong to a separate radiation that

deserves recognition as a distinct genus. Uncertainty also surrounds *Lamellitrochus*, which Quinn (1991) proposed as a distinct genus-level entity. Marshall (1999), on the other hand, suggested that *Lamellitrochus* is synonymous with *Zetela*. To date, no samples of *Lamellitrochus* have been included in any molecular systematic studies and the status of this taxon remains to be established. It is important that this is rectified in future studies.

Included species:

- Zetela annectens* Marshall, 1999;
- †*Z. avamoana*, Laws 1939 (used to calibrate molecular clock by Williams *et al.*, 2013);
- **Z. kopua* Marshall, 1999;
- ?*Z. semisculpta* (von Martens, 1904);
- Z. tabakotani* (Poppe, Tagaro & Dekker, 2006);
- Z. textilis* (Murdoch & Suter, 1906);**
- ?*Z. turbynei* (Barnard, 1963);
- Z. variabilis* Dell, 1956;
- **Zetela* spp. 1, 2 and 3 of Williams *et al.* (2013).

Species assigned to *Lamellitrochus* (taxonomic status uncertain):

- Lamellitrochus bicoronatus* (Quinn, 1991);
- L. cancapae* (Vilvens & Swinnen, 2007);
- L. carinatus* (Quinn, 1991);
- L. fenestratus* (Quinn, 1991);
- L. filusos* (Quinn, 1991);
- L. incertus* (Quinn, 1991);
- L. lamellosus* (Verrill & S. Smith, in Verrill, 1880);
- L. pourtalesi* (Clench & Aguayo, 1939);
- L. suavis* (Quinn, 1991).

Solariellid species of uncertain generic status

(Fig. 12E, 14)

The following species were included in recent molecular systematics studies, but their status with regard to the genera discussed in this study is uncertain (Williams *et al.*, 2013; Sumner-Rooney *et al.*, 2016). Additional morphological data (outlined below) and new, unpublished molecular systematic data suggest they may belong to new genera.

- *'*Bathymophila*' sp. 18 Sumner-Rooney *et al.*, 2016;
- *'*Machaeroplax*' *delicatus* (Dall, 1919);
- *'*Solariella*' *varicosa* (Mighels & C.B. Adams, 1842);
- *'*Suavotrochus*' sp. Williams *et al.*, 2013.

Remarks: Morphological evidence suggests that '*Solariella*' *varicosa* Mighels & Adams, 1842 (Fig. 14B) does not belong in *Solariella* as its radula lacks latero-marginal plates (Warén, 1993); on its own this is not completely convincing because these plates may be difficult to observe as they sometimes stick to the marginal teeth. Additional evidence from molecular systematic data not only confirm that this species does not belong in *Solariella*, but also indicate that it does not belong in any currently recognized genus (Williams *et al.*, 2013). '*Solariella*' *varicosa* also differs from most solariellids by having only three spiral threads on the protoconch, a condition shared with '*Solariella*' *obscura*.

The overall shell shape and presence of a callus would place '*Bathymophila*' sp. 18 (Fig. 14A) in *Bathymophila* s. s., but it lacks calcareous granules on the callus and is genetically distinct from *Bathymophila* (although its relationships with *Bathymophila* and other clades were poorly supported; Sumner-Rooney *et al.*, 2016). Further work is needed to see if it represents a new genus.

'*Machaeroplax*' *delicatus* (Fig. 14C) and '*Suavotrochus*' sp. (Fig. 12E) are deep-water species collected off Japan and additional, unpublished molecular systematic data for multiple specimens suggest that they belong to new and as yet undescribed genera (YK, STW).

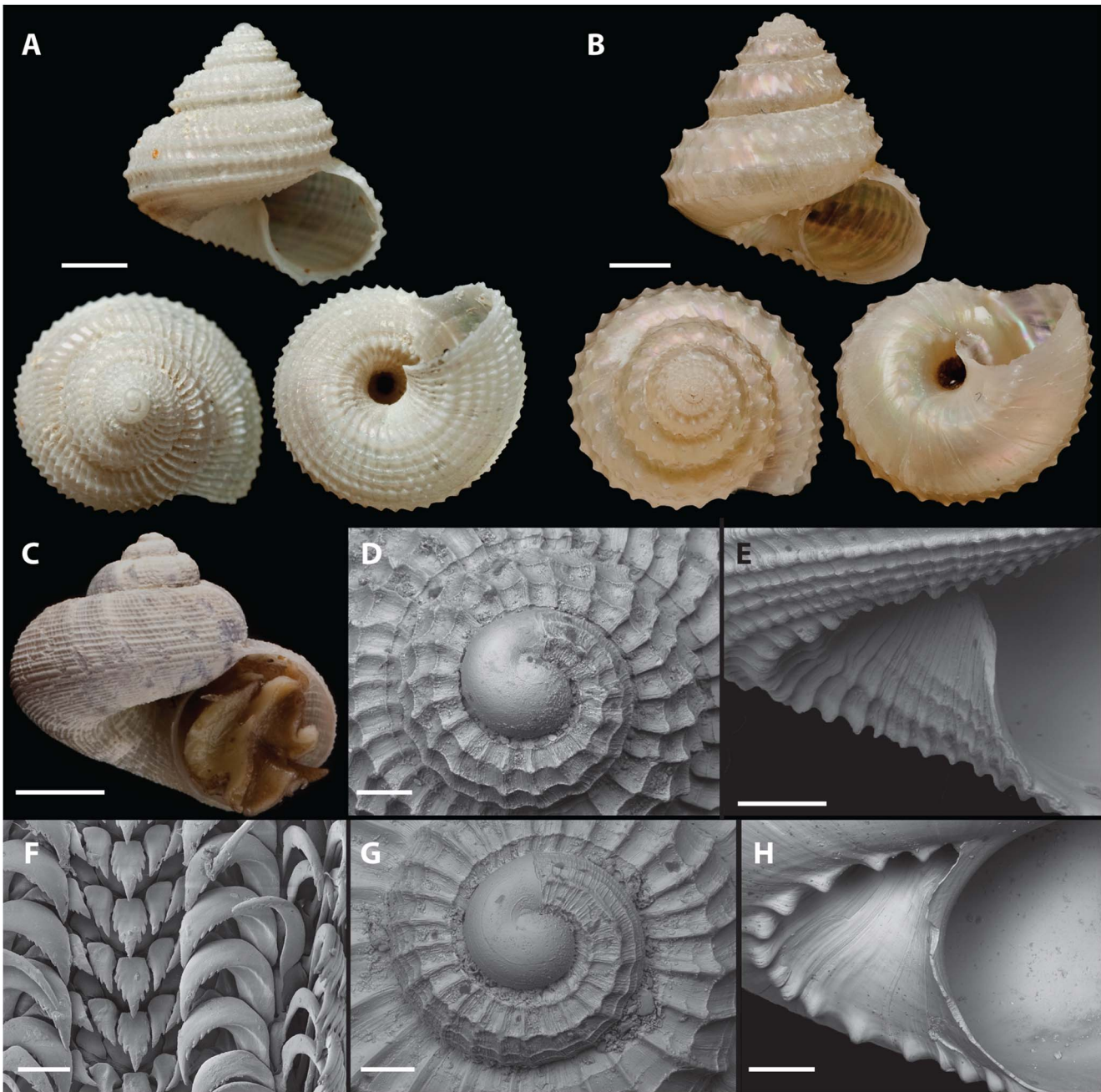


Figure 13. *Zetela* species. **A.** Type species of *Zetela*, *Zetela textilis* (Murdoch & Suter, 1906). Not used in molecular systematic studies. NMNZ M066560: NW of Mayor Island, New Zealand, 37°11.50'S, 176°10.00'E, 198–273 m. Scale bar = 1 mm. **B.** *Zetela* sp. 1 used in study by Williams *et al.* (2013). MNHN IM-2009-8748: MAINBAZA, CP3138, Maputo transect, Mozambique Channel, 25°13'S, 35°21'E, 700–707 m. Scale bar = 2 mm. **C.** *Zetela* sp. 3 used in study by Williams *et al.* (2013). NHMUK 20120240: Burdwood Bank, Antarctica. 286–290 m. Scale bar = 5 mm. **D, E.** *Zetela textilis*. NMNZ M066560: RV Tangaroa, NW of Mayor Island, New Zealand, 37°11.50'S, 176°10.00'E, 198–273 m. **D.** Protoconch and early whorls. Scale bar = 150 μ m. **E.** Detail of columella. Scale bar = 450 μ m. **F.** *Zetela* sp. 1. Radula; note the absence of a latero-marginal plate. MNHN IM-2009-15169: MAINBAZA, CP3138, Maputo transect, Mozambique Channel, 25°13'S, 35°21'E, 700–707 m. Scale bar = 50 μ m. **G–H.** *Zetela* sp. 1. MNHN IM-2009-8748: **G.** Protoconch and early whorls. Scale bar = 150 μ m. **H.** Columella. Scale bar = 750 μ m. Photo credits: H. Taylor. SEM credits: STW and DGH.

The overall shell shape of '*Suavotrochus*' sp. is remarkably similar to *Suavotrochus* s. s. and the shell sculpture on '*M.* *delicatus*' is similar to some *Zetela*, but the molecular systematic data indicate these two species are not referable to these genera (Williams *et al.*, 2013).

DISCUSSION

In this study, we have brought together information from a range of sources both historical and recent, providing a new, updated

assessment of solariellid systematics. This assessment is based on both molecular systematic data and morphological (particularly shell, radula and eye) characters. Shell characters are shown to be very useful at the generic level, with the sculpture of the early teleoconch and umbilical region, the shape of the columella and the deposition of calcareous granules being particularly valuable. It is important to note that such characters require detailed examination, often with SEM to identify all pertinent characters as overall shell shape on its own can be misleading. The problem

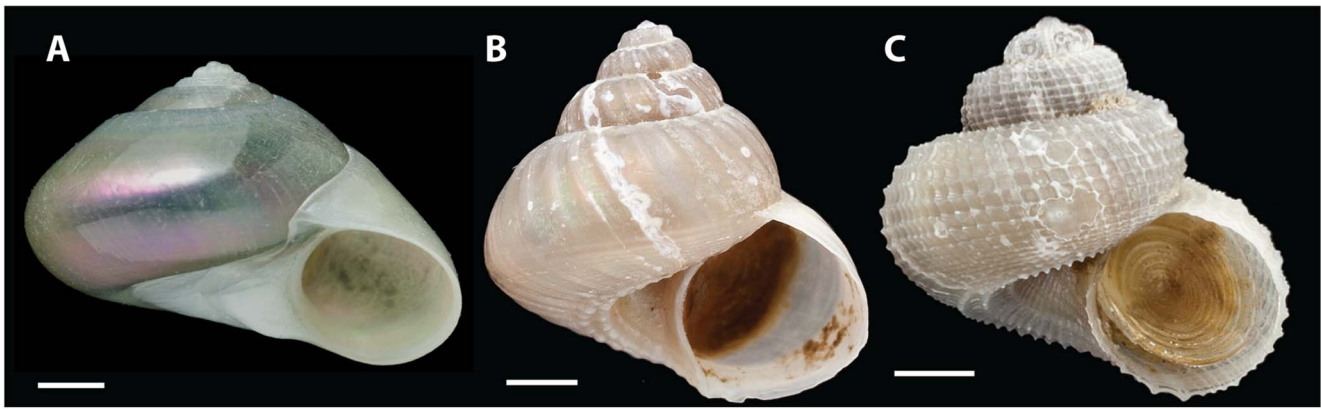


Figure 14. Species included in molecular phylogenetic studies, but of uncertain generic status. **A.** ‘*Bathymophila*’ sp. 18 of Sumner-Rooney *et al.* (2016). MNHN IM-2009-23080: Ile Matthew-Volcan, New Caledonia, 22°19’S, 171°20’E, 925 m. Scale bar = 1 mm. **B.** ‘*Solariella*’ *varicosa*. NHMUK 20120235: Finnmark County, Varangerfjorden, SW of Vestre Jakobselv, Norway, 70°4’N, 29°12’E, 10–174 m. Scale bar = 1 mm. **C.** ‘*Machaeroplax*’ *delicatus*. NHMUK 20191342: off Cape Toi, Miyazaki, Kyushu Is., Japan; 31°07’N, 131°39’E, 1,063–1,082 m. Scale bar = 1 mm. Photo credits: H. Taylor.

with overall shell shape is exemplified by the conchologically similar but genetically distinct Caribbean *Suavotrochus* and Japanese ‘*Suavotrochus*’ sp. In general, radular characters show a high level of congruence with molecular systematic data; this is particularly with regard to the presence or absence of latero-marginal plates. However, it is important to bear in mind that the latero-marginal plate is formed by the basal part of what probably equates to the fifth lateral tooth and that some genera (e.g. *Chonospeira* n. gen., *Minolia*) exhibit an intermediate condition, where the more apical part of this tooth (i.e. its shaft and cusp) may remain in a reduced or vestigial state and may break off due to wear and tear of the radula. The latero-marginal plates may also be difficult to observe in some species. Features of eye morphology are sometimes variable within genera, but major characters, such as the lack of pigmentation and loss of aperture, are informative. There is evidence that other external anatomical characters may vary amongst groups (e.g. number of epipodial tentacles, shape and form of neck and epipodial lobes; Herbert, 1987; Marshall, 1999), but at present, we lack sufficient data to fully evaluate these at the generic level.

In the majority of cases, the data on which our decisions are based are robust, and we are confident that these genera are adequately circumscribed. In particular, we are confident that *Arxellia*, *Ilanga*, *Chonospeira* n. gen., *Elaphriella*, *Minolia* and *Phragmomphalina* n. gen., all of which have been represented in molecular systematic studies by their respective type species, are well delimited. In contrast, the nominotypical genus is one of the genera for which our results are more tentative. The assignment of the name *Solariella* to a clade will always be confounded by the fact that the type species is a fossil and as such we cannot include it in molecular phylogenetic studies or examine its anatomical characters. Our current clade includes *S. amabilis* (form *affinis*), which we consider to be representative of the genus. Even if later studies show that *S. amabilis* and *S. affinis* are not synonymous, as both *affinis* and *amabilis* share shell characters consistent with our diagnosis for *Solariella*, we would not expect any changes to the taxonomic decisions made here. Ideally, both forms should be included in future molecular systematic studies; optimally the West African *S. inoptanda* should also be included as a proxy for *S. maculata* (i.e. to ensure that our assignment of *Solariella* is correct), as this species is likely to belong to the same evolutionary lineage as *S. maculata* (e.g. Bouchet, 1981) (but see caveat above about radular characters).

Other genera that remain somewhat problematic are *Bathymophila*, *Zetela* and *Spectamen*. For both *Bathymophila* and *Zetela*, we lack DNA sequence data for the type species. Moreover, for *Zetela*, we have very few tissue samples and morphological characters tend to be more variable (particularly in the case of the radula,

columella and early shell sculpture) than in other genera examined in this study, suggesting the possibility that *Zetela*, as defined here, may not be monophyletic. A further potential issue is the putative synonymy of the Caribbean *Lamellitrochus* with *Zetela*; this remains to be investigated using a molecular systematic approach.

Our current understanding of *Spectamen* is based on the morphological characters of the type species and on molecular systematic analyses, which have included specimens very similar in appearance to the type species. These analyses have provided strong evidence that *Spectamen* is a robust clade with consistent morphological characters. However, our coverage of the genus from a molecular systematic perspective is limited and does not adequately encompass the geographical range identified for this genus by Herbert (1987). Future molecular phylogenetic studies should include specimens from southern Africa to establish whether these species form a potentially endemic radiation that is distinct from *Spectamen*, which is otherwise known only from Australia and the Western Pacific. Additionally, Australian and New Zealand species with turbinata shells should also be included as the molecular systematic work carried out to date has only included species with conical shells.

Further work is also required to confirm whether new genera have to be erected for four species: the Japanese ‘*Machaeroplax*’ *delicatus*, Atlantic ‘*Solariella*’ *varicosa*, Japanese ‘*Suavotrochus*’ sp. and New Caledonian ‘*Bathymophila*’ sp. 18. All four taxa may represent distinct lineages that merit recognition as separate genera. Further molecular systematic studies including additional samples from the Atlantic, East Pacific, northwest Africa, Japan, Australia and New Zealand are needed to address these issues, to test hypotheses related to the synonymies proposed above and to better explore global solariellid diversity.

To date, the generic assignment of solariellid species has been problematic and inconsistent. Prior to studies on the molecular systematics of this group, > 200 names had been proposed for Recent solariellid species and many new species have been discovered on recent MNHN expeditions (e.g. Poppe, Tagaro & Dekker, 2006; Vilvens, 2009; Vilvens *et al.*, 2014; Vilvens & Williams, 2016; Vilvens & Williams, 2020). This study will aid in the reevaluation of many of these taxa, leading to a better understanding of diversity in Solariellidae, opening up new avenues for exploration of historical biogeography and evolutionary processes in the deep sea.

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